The effect of shoot heterogeneity on the physiology and grape composition of Shiraz/Richter 99 grapevines

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DECLARATION

I, the undersigned, hereby declare that the work contained in this thesis is my own original work and that I have not previously in its entirety or in part submitted it at any university for a degree.

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SUMMARY

The effect of shoot heterogeneity on vegetative and reproductive growth parameters, vine physiology and grape composition was investigated in a Shiraz/Richter 99 vineyard. Comparisons between underdeveloped (typically shorter and less ripened at véraison) and normally developed shoots in both shaded (non-manipulated) and well-exposed (manipulated) canopies were made. Compared to underdeveloped shoots, normal shoots had a larger total leaf area, due to the higher occurrence of secondary shoots as well as larger leaves on primary and secondary shoots. Since the photosynthetic activity of the leaves from normal shoots was higher than those from underdeveloped shoots, higher levels of carbohydrates were produced and stored in the former. Starch was more evenly distributed over the length of the whole shoot in normally developed shoots compared to underdeveloped shoots. Normally developed shoots were longer and thicker in diameter than underdeveloped shoots. The larger clusters of the normally developed shoots are evidence of their more favourable total leaf area per gram berry mass. Berries from the normally developed shoots were smaller at five weeks after véraison than those from underdeveloped shoots, displaying a higher skin to pulp ratio and therefore higher anthocyanin and total phenolic extraction potential for winemaking. The smaller clusters and fewer berries per cluster found for the underdeveloped shoots indicate an imbalance between vegetative and reproductive growth initiated during the vegetative growth phase and continued during the ripening period.

The peculiar absence of statistically significant differences in grape composition between normally and underdeveloped shoots indicates that assimilates needed for berry ripening of the latter originated in organs other than the leaves [e.g. from adjacent normal shoots and the rest of the permanent structure of the vine (cordon, trunk, roots)]. The larger differences in berry size that occurred between shoot types in the shaded compared to the well-exposed canopies may be evidence for this. The photosynthetic activity of shoots was lower in shaded than in exposed canopies. The total carbohydrate production of the normal shoots in shaded canopies seemed insufficient to supply in the ripening needs of the shoot itself, their own clusters as well as the ripening of stem tissue and clusters of the underdeveloped shoots in the canopy. This is illustrated by the lower levels of starch that accumulated in the normal shoots from shaded compared to that of exposed canopies. Vine shoot heterogeneity clearly leads to visible and physiological imbalances that would impact negatively on grape and wine quality as well as production costs and should therefore be avoided on any terroir.

OPSOMMING

In hierdie studie is die effek van heterogene lootontwikkeling in die lower van 'n Shiraz/Richter 99 wingerd ondersoek. Vergelykings is getref tussen normale en onderontwikkelde lote in beskadude en blootgestelde lowers ten opsigte van hul vegetatiewe en reproduktiewe groei-eienskappe, fisiologiese aktiwiteit en druifsamestelling en –gehalte. 'n Groter totale blaaroppervlak het by die normaal ontwikkelde lote voorgekom as gevolg van die groter aantal sekondêre lote en groter primêre en sekondêre blare. Aangesien die blare van die normaal ontwikkelde lote fotosinteties meer aktief was as dié van onderontwikkelde lote, het die eersgenoemde lote groter hoeveelhede koolhidrate geproduseer en gestoor. Styselopberging het meer eweredig oor die lengte van die normale lote plaasgevind. Laasgenoemde lote was ook heelwat langer en dikker in deursnee as die onderontwikkelde lote. Die gunstiger totale blaaroppervlak per korrelmassa verhouding van die normale lote is duidelik weerspieël in die groter trosse, terwyl die kleiner korrels (en dus die groter dop:pulp verhouding) op 'n groter potensiaal vir kleur- en fenolekstraksie tydens die wynbereidingsproses dui. Die kleiner trosse en kleiner aantal korrels per tros wat by die onderontwikkelde lote gevind is, dui op 'n wanbalans tussen die vegetatiewe en reproduktiewe groei van die loot wat tydens die vegetatiewe groeifase van die wingerdstok geïnisieer is en tydens die rypwordingsperiode voortgesit is.

Die vreemde afwesigheid van enige statisties betekenisvolle verskille in druifsamestelling tussen die normale en onderontwikkelde lote dui daarop dat die verbindings wat vir die rypmaking van trosse op onderontwikkelde lote aangewend is, waarskynlik van ander wingerdorgane (bv. naasliggende lote, kordonarms, stam, wortels) as die spesifieke loot se blare afkomstig was. Die waarneming dat die korrelgroottes van normale en onderontwikkelde lote meer van mekaar verskil het in die beskadude as blootgestelde lowers, kan moontlik as bewys hiervoor dien. Die fotosintetiese aktiwiteit van beide loottipes was laer in die skaduryke lowers. Die koolhidrate wat deur normaal ontwikkelde lote in skadu-lowers geproduseer is, was oënskynlik onvoldoende vir die rypmaking van die loot self, die spesifieke loot se trosse, asook die trosse en lootweefsel van naasliggende onderontwikkelde lote. Hierdie bewerings word gerugsteun deur die laer vlakke van styselakkumulasie wat by die normale lote in beskadude lowers gevind is. Aangesien heterogene lootontwikkeling en –groei duidelike sigbare en fisiologiese wanbalanse in die wingerdstok tot gevolg het wat negatief op druifsamestelling, wyngehalte en produksiekoste inwerk, behoort dit in kommersiële wingerde vermy te word.

This thesis is dedicated to my parents.

BIOGRAPHICAL SKETCH

Hanlé Cloete grew up in Paarl and attended Gymnasium High where she matriculated in 1997. She then studied Viticulture and Oenology at the University of Stellenbosch, South Africa, where she received her BScAgric degree in 2001. She is currently employed by the Cape Technikon where she teaches Viticulture and Oenology at their Wellington campus.

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PREFACE

This thesis is presented as a compilation of eight chapters. Each chapter is introduced separately and is written according to the style of the *South African Journal of Enology and Viticulture*.

CHAPTER 1

INTRODUCTION AND OBJECTIVES OF STUDY

With its wet winters and long, hot summers, the climate of the Western Cape is favourable for vegetative growth of the vine. With improved cultivation practices and better propagation material, the potential for vine vigour and shaded canopies increases.

Research has shown that a too dense canopy is detrimental to the physiological functioning of the vine. Koblet (1987) stated that the largest microclimatic difference between dense and sparse canopies is the radiation flux density. As the photosynthetic efficiency of individual leaves, and per implication photosynthesis of the whole vine, is closely linked to the amount and intensity of sunlight interception (Hunter, 1991), a canopy where all the leaves are sufficiently exposed to sunlight is essential to maximise the vegetative and reproductive growth of the vine.

Canopy shade was associated with delayed grape maturation (Archer, 1988; Smart *et al.*, 1988; Smart *et al.*, 1989; Keller & Hrazdina, 1996). Rojas-Lara & Morrison (1989) found that shaded canopies led to delays in both berry growth and ripening. Jackson & Lombard (1993) linked excessive shading to juice with unbalanced composition, which resulted in poor wine quality. According to Smart (1982) canopy shade significantly reduced red wine quality in hot areas. It is important that the canopy is managed in such a way that the photosynthetic capacity of the vine and the ripening of the grapes are favoured.

Canopy management practices during the growth season are aimed at changing the magnitude, position, and/or orientation of canopy components (shoots, leaves and clusters), improving the microclimate (light, humidity, air flow, temperature) and balancing the vegetative (including the roots) and reproductive development and functioning (Hunter & Archer, 2001). Carbon allocation to fruit sinks can thus be optimised (Hunter, 2000) without detrimentally affecting growth and development in other parts of the grapevine so that longevity can be maintained (Hunter & Archer, 2001).

The eventual objective of canopy management is to obtain a photosynthetic efficient, homogeneous canopy with uniformly and well distributed shoots of similar vigour, producing healthy, high quality grapes of similar bunch and berry size and with a uniform level of ripeness (Hunter & Archer, 2001). Where large variation in berry composition in a vineyard exists, the potential for the presence of overripe and unripe flavours in the must and wine is increased, even though

the average composition may seem acceptable (Trought, 1996). According to Smart *et al.* (1990) high quality wines result from processing fruit of relatively similar composition.

Research done on the effect of canopy management showed that the treated vines had a uniform interception of sunlight throughout the whole canopy, which led to a more homogeneous ripening of all the clusters (Volschenk & Hunter, 2001). Apart from the effects of irregular sunlight exposure, asynchronous ripening may be enhanced by the varying leaf area:fruit ratio of individual shoots (Jackson & Lombard, 1993). Short shoots may have insufficient leaf area to adequately ripen their clusters (Peterson & Smart, 1975). Koblet (1977) found that short shoots imported more assimilate from adjacent shoots than did normally developed shoots. It can be assumed that the presence of short shoots may lead to a decrease in the grape quality of other, stronger shoots on the same vine. Different shoot lengths in a vine would thus impair the overall quality (Archer, 2001), as well as increasing the variation in composition of individual clusters. Equality in shoot growth seems important for the production of homogeneous, top quality grapes.

The purpose of this study was to investigate the effect of shoot heterogeneity in a Shiraz/Richter 99 vineyard on vegetative and reproductive growth parameters, vine physiology and grape composition.

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CHAPTER 2

LITERATURE REVIEW

THE EFFECT OF SHOOT HETEROGENEITY ON GRAPEVINE PHYSIOLOGY AND FRUIT COMPOSITION

CONTENTS

1. VEGETATIVE GROWTH

The start of a new growth cycle for *Vitis vinifera* commences at bud break. At the onset of warmer temperatures, acceleration of metabolic activity takes place, with the resulting bud break, shoot growth, flowering, véraison and ripening of grapes and shoots.

1.1 SHOOT DEVELOPMENT

According to Coombe (1992a), grapevine shoots in general initially grow slowly after bud break followed by a massive growth of vegetative tissue during late spring. This growth includes both the expansion of existing leaves and internodes and the production of new organs (Pratt, 1988). In late summer the main shoots grow at a slower rate, while internode elongation ceases progressively from the basal to the apical part of the shoot. Ideally, according to Archer (1988), shoot growth should stop at véraison in a balanced vineyard. De la Harpe (1983) described the shoot growth of *Vitis vinifera* cv. Cape Riesling to be sigmoidal.

Shoot length (and vigour) determined the number of primary leaves and secondary shoots per vine (Dokoozlian & Kliewer, 1995). The ratio of the leaf area to shoot length was used as an index of shoot leafiness by Smart (1992) and was found to be vigour dependent, being larger for more vigorous shoots. In vigorous vines, assimilates were mostly translocated to the vegetative parts of the vine, while the clusters were neglected (Hunter, 1991). The consequences may be an increased shoot growth and leaf area, as well as the appearance of too many secondary shoots, water shoots and the outbreak of basal buds. The result being a high shoot density with reduced aeration and elevated humidity, low penetration of fungicides, shading of shoots, developing buds, basal leaves and clusters and poor cane ripening (Reynolds *et al.*, 1986a; Hunter, 1991; Jackson & Lombard, 1993).

Increased node numbers retained at winter pruning and increased crop load per shoot proved to be natural ways to induce shoot devigouration in otherwise vigorous vines (Smart *et al.*, 1989). Hunter & Visser (1990a) found that partial defoliation slightly reduced the main shoot length, but the vine compensated by increasing the number of secondary shoots and the mean secondary shoot length. An increase in the total shoot length per vine was thus found.

Van Zyl (1981) noted that reduced shoot growth during the early growth season could be an indication of water stress, while according to Bravdo (2000), regulated water deficit at the early phase of vegetative growth could be used as a tool to reduce high vigour. Moderate water deficit after véraison also would inhibit further vegetative growth (Bravdo, 2000), as Van Zyl (1981) found that shoot growth would continue (although at a lower rate) through the whole season in the presence of adequate water. According to Myburgh (1998), Williams *et al.* (1994) stated that severe water deficits induced by insufficient irrigation may result in poor vegetative growth, economically unviable production and unacceptable grape quality.

A too dense canopy can easily be identified by certain shoot characteristics. Hunter (1991) and Keller & Hrazdina (1996) found that low light intensities stimulated shoot growth with longer than usual internodes as a result. Archer (1988) observed light green, growing shoot tips between véraison and ripeness, while Hunter (1991) reported more than 50 percent active shoot tips, which included many and long actively growing secondary shoots. A large proportion of short, self-terminating shoots were also found in the canopy interior, where they developed from latent and collar buds (Smart, 1988).

Smart *et al.* (1985a) and Smart *et al.* (1989) concluded that it is mainly shoot density that is unfavourable to grape yield and quality, as shoot length as such showed limited or no correlation with must and wine composition (Smart *et al.*,

1985b). In direct contrast, Archer (2001) found that shoots of a medium length (±120 cm) produced the best grapes for making quality wine, compared to the sub-optimal ripening of grapes (and thus poorer wine quality) in the case of long (>200 cm) and short (±60 cm) shoots. In a study where the effect of the training system height (and the shoot length) on the quality of Cabernet Sauvignon grapes and wine was determined, Nadal *et al.* (2001) found that grapes from shoots with an average length of 145 cm produced wines with higher tannin, anthocyanin and alcohol content than grapes from 110 cm shoots. This result was ascribed to the better foliar exposure (m^2/ha) of the higher training system, as no difference in canopy density between the treatments was found.

McCarthy (1996) stated that high quality wine generally came from vines with a moderate vigour and comparable little secondary shoot growth where the shoots had slowed or stopped elongating around véraison.

1.2 LEAF DEVELOPMENT AND FUNCTION

Leaf development of the grapevine follows a well-defined sequence of emergence, unfolding and rapid laminar expansion, followed eventually by senescence and abscission (Kriedemann *et al.*, 1970). Grapevine leaves showed a typical sigmoid growth curve (De la Harpe, 1983), with the rapid growth phase occurring in the second and third weeks after unfolding. The leaf attained its full size about four weeks after its growth had started (Hale & Weaver, 1962).

According to Hale & Weaver (1962), export of assimilates started when the leaf reached about half its final size (as determined by leaf position and growth conditions), but Koblet (1977) stated that leaves began to export photosynthetic products at about 30 percent of their mature size (leaves from the main as well as the secondary shoots), although the import of assimilate from larger leaves was still continuing. As soon as the leaves reached 50 percent (main shoot) and 75 percent (secondary shoot) of their final size, only an export of assimilates

occurred. The maximum photosynthetic activity (and thus export) was achieved as the leaf reached full size about 30 to 40 days after unfolding, whereafter a gradual decline in the rate of photosynthesis was noted (Kriedemann *et al.*, 1970).

Changes in CO_2 compensation point (hence carboxylation efficiency and photorespiration), plus alterations in internal anatomy, seemed related to the increased photosynthetic activity with leaf expansion. Old leaves showed a reduction in both efficiency and capacity, which was associated with a substantial increase in internal resistance to CO_2 assimilation (Kriedemann, 1977). At the end of berry ripening there was almost no export of assimilate from the older, basal leaves (Koblet, 1977), although it was found that even leaves of four to five months old with visible signs of senescence still achieved a photosynthetic rate of 1,1 $mg.dm^{-2}.h^{-1}$ *in situ* under field conditions (Kriedemann *et al.*, 1970). The stable, ongoing photosynthetic activity of basal leaves up to harvest and thereafter, indicated a continued competence to support the clusters and contribute to maintenance metabolism of the vine (Hunter *et al.*, 1994). During its development, the vine leaf is therefore characterized by changes in morphology, anatomical detail, pigment concentration and the products formed during CO_2 fixation (Kriedemann, 1977).

There was an increase in leaf area per shoot from bud break to véraison, followed by a decline (Hunter & Visser, 1990a). This leaf area was found to be dependent on the vigour – vigorous shoots had more and larger leaves, especially on the secondary shoots (Smart, 1984).

Dokoozlian & Kliewer (1995) observed a close correlation between the leaf area density (expressed as leaf area per vine; leaf area per metre canopy length; leaf area per vine divided by the total ground area allotted to each vine; leaf area per vine divided by the ground area covered by the vine canopy and/or leaf area per vine divided by the canopy surface area per vine) and the evaporative potential in

the fruit zone. Smart (1984) found that the potential for humidity build-up in dense canopies due to a reduced wind velocity, was not realised because of the reduction of the transpiration rate of the interior leaves due to shading and low overall evaporation rates within dense canopies.

Stimulated vigour of the vine increased the total leaf area, which led to an increase in interior canopy shade (Smart *et al.*, 1985a). As the leaf area density increased, the PPFD (Photosynthetic Photon Flux Density) decreased (Dokoozlian & Kliewer, 1995). Keller & Hrazdina (1996) found that low light intensity stimulated individual leaf area expansion. According to Kappel & Flore (1983), an increased leaf area may lead to an increase in the effective light interception area. This does not always seem to be the case in practice, because although there is a potential increase in the total light interception area, there is not necessarily an increase in the effective leaf area due to leaf density and shading in the canopy. Kappel & Flore (1983) also found that shading decreased the specific leaf mass, while Marini & Marini (1983) noticed a strong positive correlation between the specific leaf mass and PAR (Photosynthetic Active Radiation) in the canopy.

Shade conditions could readily be recognized in vineyards by yellowing of especially interior basal leaves (Archer, 1988; Hunter, 1991), as well as their premature abscission (Smart, 1982; Archer, 1988). Archer & Strauss (1989a) found that light intensities around 20-30 $\mu E.m^{-2}.s^{-1}$ led to the early yellowing of leaves. Such leaves made no contribution to the photosynthetic capacity of the vine.

It was found that water stressed vines had more or less the same symptoms than light stressed vines – leaf senescence already began one month before véraison (Vicente-Paulo *et al.*, 2000), with abnormal early abscission (Van Zyl, 1981). The resultant reduced active leaf area relatively early in the season can have various negative consequences, such as premature reduced shoot growth, ripening of

shoots and clusters, and bud break in the following season (Van Zyl, 1981, and references therein). In drying soils, it was further found that roots chemically inhibited the initiation and expansion of leaves, even when the shoots were still well supplied with water and the leaves had yet to lose turgidity (Davies & Zhang, 1991). This inhibitive function of the roots could be the reason why Van Zyl (1981) reported the development of smaller leaves under conditions of water stress. Differences in the size and amount of stomata, leaf anatomy and thus physiological functioning of these leaves may also be expected.

Vaadia & Kasimatis (1961) found that under conditions of extreme water stress, leaves changed their orientation parallel to the sun under high temperatures (Van Zyl, 1981). This is probably a way to reduce water loss by transpiration while extending the active photosynthetic period. According to Kasimatis (1967), Veihmeyer & Hendrickson (1950a) concluded that the drought resistance of the vine is not due to an inherent ability to extract more water out of dry soil, but rather to the ability to balance the amount of water taken up by the roots and the amount transpired by the vegetative organs. In this way normal physiological functions of the vine can continue, albeit at a lower rate.

1.2.1 Chlorophyll

The photosynthetic light absorbing pigment embedded in specialised internal membranes (called the thylakoid system) in the chloroplasts, is called chlorophyll. Two kinds of chlorophyll can be distinguished, namely chlorophyll *a* (blue-green) and chlorophyll *b*, which is yellow-green in colour (Salisbury & Ross, 1992). The content of chlorophyll *a* is usually two to three times that of chlorophyll *b*, and according to Hunter & Visser (1989), Sestak (1966) stated that chlorophyll *a* was considered a more exact indication of photosynthetic activity potential.

Although the chlorophyll concentration reached a peak when the leaf achieved maximum photosynthetic activity (approximately 40 days after unfolding), the

chlorophyll concentration remained constant during the initial expansion phase (Kriedemann *et al.*, 1970) when an increase in photosynthetic activity of the leaf took place. Therefore some factors other than the chlorophyll concentration were responsible for the increased photosynthetic activity. Anatomical changes during leaf expansion (lower resistance to CO_2) would stimulate the influx of CO_2. Also, a higher demand for photosynthetic products could have affected the rate of CO_2 assimilation in the vine (Kriedemann *et al.*, 1970). Hunter & Visser (1989) found no consistent relationship between chlorophyll concentration and photosynthetic activity of exterior leaves. Thus the chlorophyll content should not be regarded as a reliable index of photosynthetic activity. Hunter & Visser (1989) further stated that factors such as the source:sink relationship, competition between leaves for mineral nutrients and hormones, feedback inhibition of photosynthesis by end products and enzymes involved with carboxylation in chloroplasts, as well as internal resistance to CO_2 transfer within the leaf, were probably more regulatory to photosynthetic activity than chlorophyll concentration and light intensity. However, a relationship was found between the chlorophyll concentration and the photosynthetic activity for mature, interior canopy leaves that were exposed to lower light conditions (Hunter & Visser, 1989).

According to Kappel & Flore (1983), the chlorophyll content of peach tree leaves that were formed in the shade increased as the light intensity decreased. The chlorophyll *a*:chlorophyll *b* ratio was however unaffected. Marini & Marini (1983), as well, found that interior leaves of peach trees tended to have significantly higher chlorophyll *a*, chlorophyll *b* and total chlorophyll content than peripheral leaves. In the case of *Vitis vinifera*, Hunter & Visser (1989) also found an increase in the total chlorophyll concentration for the interior, recently matured leaves, but a decrease in the chlorophyll *a* concentration as the leaves were progressively situated deeper into the canopy.

1.2.2 Light

The wavelengths between 400 nm and 700 nm that is capable of causing photosynthesis in plants, is called Photosynthetic Active Radiation (PAR) (Salisbury & Ross, 1992), also known as Photosynthetic Photon Flux Density (PPFD). Marini & Marini (1983) found that PAR penetration in the canopy decreased as the season progressed, due to normal shoot elongation. Smart (1984) also found that the PAR levels declined with passage through successive leaves from the canopy surface. Shorter wavelengths are more important than the longer wavelengths, but get easier diffused. The result being that the leaves in dense canopies receives mostly light with longer, less functional wavelengths (Archer, 1988).

Phytochromes are proteinaceous pigments that are associated with light absorption. There are two stable forms, namely P_{red}, which is blue in colour and absorbs red light (maximum 667 nm) and $P_{far\text{-}red}$, which is greenish is colour and absorbs the far-red (maximum 724 nm) light. When either form absorbs light, it is converted to the other. As $P_{far\text{-}red}$ is considered to be the active form of the pigment, R:FR ratio of the radiation flux is also regarded as important. The active phytochrome pigments play a role in several aspects of plant development, e.g. photoperiodism (initiation of flowering and certain vegetative activities of plants in response to relative lengths of day and night), changes in plastids, germination of seeds, production of anthocyanins and detection of shading and modifying growth accordingly (Hunter, 2001). Although not yet proven in grapevine, it could be accepted that phytochrome plays a significant role in development, adaptation and transmitting information from the environment to the vine. It had been shown that the functioning of several critical enzymes is controlled by phytochrome activity, which includes phenylalanine ammonia lyase (PAL), RubisCo (ribulose bisphosphate carboxylase/oxygenase), nitrate reductase and malate dehydrogenase. There exist only a few enzymes that are apparently not being controlled by P_{fr} (Schopfer, 1972). However, no

clear evidence has been found that phytochrome plays a role in fruit colouration and ripening in the grapevine (Hunter, 2001).

According to Smart (1984) and Dokoozlian & Kliewer (1995), both PPFD and R:FR declined sharply in the fruit zone as canopy density (defined elsewhere) increased. A positive linear relationship between these two parameters was found in the fruit zone. Koblet (1987) stated that the largest microclimatic difference between dense and sparse canopies proved to be the radiation flux density.

Smart (1987) also found a linear relationship between the solar radiation and temperature. Shading, according to Klenert (1975), resulted in a reduction of solar radiation, with the resultant decrease in air, soil and vine temperatures during the day. Jackson & Lombard (1993) stated that higher radiation (be it intensity or duration) increased the temperature of especially exposed leaves and berries, which led to an increased photosynthetic and metabolic activity in these organs.

Thus sunlight can affect fruit composition through photosynthetical, phytochromal, as well as thermal effects (Smart, 1987).

1.2.3 Photosynthesis

According to Kriedemann (1977), Huglin (1972) stated that the aerial environment dictates how closely vine leaf photosynthesis approaches its inherent capacity as set by genetic factors. Although genetic factors set an upper limit to photosynthetic capacity, observed rates were more commonly dictated by environmental stress or internal control. These internal control mechanisms affected overall demand for photosynthetic products and how assimilates were to be partitioned between vegetative and reproductive growth. Environmental conditions, such as light, temperature, CO_2, O_2 and moisture supply, operated within this context by determining instantaneous rates of photosynthesis.

The leaves in the canopy should be managed in such a way that their full potential is explored (Hunter *et al.*, 1991a). Individual leaves should be maximally exposed so that photosynthetic conditions can be optimal for each leaf. According to Hunter & Visser (1990b) it is essential that the leaves of the grapevine be maximally exploited to benefit the vegetative as well as the reproductive growth during the growth season.

The efficiency of the leaves was dependent on the amount and intensity of sunlight interception (Hunter, 1991). Petrie *et al.* (2000) also found that whole vine photosynthesis was closely linked to light intensity. According to Champagnol (1984) photosynthesis occurred optimally at light intensities of between 704 $\mu E.m^{-2}.s^{-1}$ and 1100 $\mu E.m^{-2}.s^{-1}$. Archer (1988) stated that, during optimal light conditions, leaves that received direct sunlight were photosynthetically the most effective. The more the leaves were exposed to PAR, the higher the rate of photosynthesis. At too high light intensities, however, the stomata closed with a resultant decline in photosynthesis. On the other hand, as shading increased, the photosynthetic rate per unit area decreased (Kappel & Flore, 1983). Caspari & Lang (1996) also found that carbon assimilation was reduced at low light intensity, whereas Hunter *et al.* (1994) stated that the decrease in ambient light intensity played a significant role in the decline of photosynthesis in the late afternoon. The photosynthetic efficiency of the leaves decreased as they were progressively situated deeper into the canopy (Hunter & Visser, 1988a; Hunter 1991). Dense canopies, due to excessive vegetative growth, led to sub-optimal interior canopy microclimate and proved to be detrimental to the photosynthetic rate of the entire canopy (Hunter & Visser, 1988b; Hunter *et al.*, 1991a).

According to Koblet (1977) leaves that were completely shaded, showed practically no export, while shade leaves that still received intermittent light over parts of their surfaces, showed an active export of photosynthetic products. This

photosynthetic activity of partially shaded leaves is considered very important under circumstances of high light intensities where the exterior leaves are no longer active due to closure of their stomata (Archer, personal communication).

Kappel & Flore (1983) found that the carbon assimilation rate of peach leaves that developed and were growing in the shade was lower than that of exterior leaves, even though the former would be operating at maximum rate. Thus, interior leaves had a lower maximum photosynthetic rate than exterior leaves, even when both were exposed to light saturation levels. It was further found that plants that developed in the shade were often more efficient than sun-exposed plants at low PAR levels. It could be that the same applies to vine leaves that developed in the canopy interior under low light intensity.

The light compensation point is the light intensity where the same amount of carbon is used during photosynthesis that is released by respiration (Salisbury & Ross, 1992). Thus, when a leaf received light at an intensity equal to, or less than, the light compensation point, no net export of carbon assimilates would take place and the leaf would no longer be able to function as a source. Kriedemann (1977) found that leaf senescence tended to occur below the light compensation point, which accounted for the high mortality of basal leaves inside dense canopies, as also reported by Smart (1982), Archer (1988) and Hunter (1991).

As previously mentioned, a linear relationship exists between radiation and temperature. Kriedemann (1977) found that temperatures between 10°C and 15°C were sub-optimal and limited the full expression of a leaf's photosynthetic potential. Caspari & Lang (1996) also found that carbon assimilation was reduced at low temperatures. Temperatures between 20°C and 25°C were found by Kriedemann (1977) to be optimum under glasshouse conditions where the leaves achieved maximum rates of photosynthesis, whereas Alleweldt *et al.* (1982) considered 25°C as optimum. Temperatures higher than the optimum had

a negative influence on enzyme activity (Hunter, 1991), while excessive temperatures could lead to the thermal instability of enzymes and tissue desiccation (Kriedemann, 1977; Hunter, 1991). It should, however, be kept in mind that the optimum temperature for photosynthesis is not necessarily the optimum temperature for growth and development of the vine (Kriedemann, 1977).

According to Petrie *et al.* (2000) the photosynthetic rate of individual leaves could be affected by leaf age and location, light levels on the leaves and the rest of the vine, total leaf area in relationship to crop load and the stage of fruit maturity. Kriedemann (1977) stated that leaves generally had the capacity to photosynthesise faster as the demand for their products increased. Hunter (1991) agreed by stating that the photosynthetic activity of a leaf was dependent on the demand of the sinks for assimilates.

The demand for assimilates, leaf age and a suitable microclimate seemed to be of the utmost importance for the leaves to reach maximum photosynthetic capacity (Hunter & Visser, 1988b). On the other hand, the leaf morphology, chloroplast structure, mesophyll resistance or the RubisCo activity may be limiting to photosynthetic rate per unit area (Kappel & Flore, 1983).

Hunter *et al.* (1994) reported a general decline in photosynthesis as the season advanced, regardless of the leaf position, while Hunter & Visser (1988a) and Archer (1990) also noticed a significant decrease in specific photosynthetic activity during the season. This decline was related to the senescence of the leaves, seasonal conditions, and changing demands of sinks (including the crop) as well as modifications in canopy and leaf exposure (Hunter *et al.*, 1994). According to Archer (personal communication), the degree of light exposure can influence the productive life span of a leaf. By exposing leaves to sunlight, the photosynthetic activity will remain longer at the maximum level compared to shaded leaves where senescence can set in even after only 30 days.

1.2.4 Transpiration

Transpiration depends on the availability of energy to vaporize water and the resistance to liquid and vapour movement in the soil-plant-atmosphere system (Smart, 1974). Light and temperature would therefore play a role in this process.

Alleweldt *et al.* (1982) reported an almost linear increase in transpiration rate from 10°C to 30°C, while Petrie *et al.* (2000) found that whole vine transpiration was closely linked to the light intensity. By measuring the hourly sap flow in the xylem, Myburgh (1998) found no linear increase with net radiation, which suggested that maximal stomatal opening only allowed a fixed amount of transpiration. A temporary decrease in sap flow rate was generally observed during the late mornings and early afternoons. This indicated a possible water saving mechanism resulting from stomatal closure under high light intensity conditions.

According to Hunter & Visser (1988b) the transpiration rates generally increased with an increase in degree of defoliation, although Myburgh (1998) found a close correlation between the transpiration and the leaf area per vine. The transpiration rate per leaf was found to decrease the deeper into the canopy the leaf was situated (Hunter & Visser, 1988b). Leaves in the centre of dense canopies received light of low flux density, enriched in the near infrared waveband. This probably explained the high stomatal resistance values found for especially the basal and bunch leaves of the control vines. Smart (1974) also reported a higher relative stomatal resistance of the shaded interior leaves due to the low levels of light within the canopy.

Escalona *et al.* (2000) found a general decline in sap flow and transpiration during the growth season, while Hunter & Visser (1988b) reported a decline in transpiration rate as the leaves aged during the course of the season.

No difference in the sap flow velocity was found after the total crop load was removed during ripening (Myburgh, 1998). It was therefore assumed that, comparing to the canopy, clusters were not strong sinks for water. Kasimatis (1967) also found that the clusters, or crop load, did not affect the amount of water needed by the vine significantly. Stomata (openings in green parts of the vine through which transpiration primarily occurs) are mainly found on leaf surfaces (Archer, 1981). Since water loss thus occurs almost entirely in the leaves, Myburgh (1998) linked the transpiration rate during grape development and ripening directly to the leaf area and functioning. However, it is important to keep in mind that water loss through berries also occurs. Ollat & Gaudillère (1995) found that berry transpiration was almost constant throughout berry development. Therefore any changes in the water balance in the vine during the season, are probably due to changes in the leaf area or functioning.

According to Archer & Strauss (1989b) stomatal resistance increased under dryland conditions as the growth season progressed, while the transpiration rate decreased. They ascribed it to increased water stress during the later stages of the season that could increase the stomatal resistance with a resultant decrease in gas exchange. It must however be kept in mind that cultivation practices, such as irrigation management, will affect leaf activity and therefore also the stomatal resistance pattern during the season.

2. REPRODUCTIVE GROWTH

2.1 BERRY DEVELOPMENT AND MATURATION

The grape berry is non-climacteric with a double sigmoid growth curve (Hunter, 1991). Staudt *et al.* (1986) found that the fresh, as well as the dry mass curves, showed a double sigmoid curve. In *Vitis vinifera* it was postulated that two phases of berry growth occur, as the so-called lag phase was not considered to be a growth phase, but rather the changeover from the first to the second growth phase. According to Coombe (1992a) fruit development has two distinct growth

cycles: the first takes the berries to the hard, green, slow growing phase, whilst the second cycle (which begins at véraison) includes the berry ripening processes. Various authors have interpreted the course of berry growth in *Vitis vinifera* differently, as divisions into two, three or four growth phases have been postulated (Staudt *et al.*, 1986). Generally, the increase in berry mass is divided into three phases: a period of rapid growth until the seed reaches mature size; a period of slow growth ending with the beginning of loss of green colour (véraison); and a period of rapid growth ending in maturity (Pratt, 1988). However, all the sources portray a double sigmoid growth curve, regardless of the way of division.

During the first growth period, the berry mainly imported carbon from source leaves. Although grape berries never exhibited net photosynthesis during their development, their photosynthetic activity was very important to decrease the amount of carbon lost through respiration (Ollat & Gaudillère, 1997). This imported carbon was then partitioned between seed growth, pericarp growth and respiration (Ollat & Gaudillère, 1995). The seeds constituted an important pool for carbon storage before véraison, since the latter source found that the carbon content of the skin and flesh remained constant, while the content of the seeds increased. Respiration represented one third of the carbon demand, which indicated that a lot of energy was required during synthesis and growth of the pericarp and seeds (Ollat & Gaudillère, 1995).

The date of véraison for a specific cultivar varies from year to year. Although there is still uncertainty in this regard, abscisic acid (ABA) was considered a possible candidate for the triggering of grape berry ripening by Coombe (1992b). A berry that had ripened earlier had no effect on the ripening of other berries on the same cluster – each berry appeared to develop independently as a separate entity.

Véraison is associated with berry softening (loss of cellular compartmentation) and volume increase (increase in cell wall elasticity) (Coombe, 1992b). Huang & Huang (2001) suggested that cell wall loosening in flesh tissues precedes cell wall loosening in skin tissues, and that this results in a two-step sequence where berry softening is followed by berry expansion.

At véraison, carbon import to the berries started to increase. The carbon was mainly translocated to the pericarp and stored as hexose (Ollat & Gaudillère, 1995; Ollat & Gaudillère, 1997). This increase in carbon import and active hexose storage during ripening did not require a lot of energy, which explained the almost ten times less respiratory costs (carbon.day^{-1}.berry^{-1}) than before véraison (Ollat & Gaudillère, 1997).

Assimilates imported into ripening berries mainly originated from recent photosynthesis in the nearby leaves (Coombe, 1992b). According to Kliewer & Antcliff (1970) vines that were completely defoliated at véraison could still ripen fruit to 14 °B, which showed the possibility that vines use carbohydrate reserves for grape maturation when stress conditions occur.

According to Coombe (1987a) the sucrose levels in unripe berries remained low, while the glucose concentration was higher than the fructose concentration. The accumulation of **sugars** was favoured at véraison (Hunter & Visser, 1988a), with glucose still as the dominating sugar (Hunter *et al.*, 1991a). It was found by Coombe (1992b) that the sugar started to increase sharply on the same day that berry softening began. The findings of Huang & Huang (2001) corresponded to that. The sugar was mainly stored in the form of hexoses in the flesh (Ollat & Gaudillère, 1997). After the considerable increase in sugar concentration, the curve tended towards a plateau (Coombe, 1992b). At ripeness, the glucose:fructose ratio strives towards one. With further ripening a decrease in the glucose:fructose ratio occurs, with the result that fructose is the dominant sugar in overripe berries (Hunter, 2001, and references therein).

After berry volume reached a peak, a further increase in sugar concentration was also associated with a loss of water from the berries. Coombe (1987a) found further increases in the concentration of several solutes in the flesh of overripe grape berries. Iland & Coombe (1988) found that leaching from the flesh became more rapid as ripening progressed, which is in agreement with the statement of Coombe (1987a). This phenomenon might suggest a gradual and general disorganization of flesh cell membranes as the berries ripen.

It was generally found that sugar accumulation in the berries was impaired in too dense canopies (Smart *et al.*, 1985b; Coombe, 1987b; Archer, 1988; Jackson & Lombard, 1993; Iacono *et al.*, 1995; Kliewer & Dokoozlian, 2000; Tomasi *et al.*, 2000; Bergqvist *et al.*, 2001). An increasing degree of shading was associated with a decrease in juice glucose and fructose concentrations, as well as the glucose:fructose ratio (Smart *et al.*, 1988).

These overall lower sugar levels were explained by the decrease in stomatal conductance under shade conditions (Iacono *et al.*, 1995) with the resultant inhibition of photosynthetic activity of the leaves (Smart, 1987). Reynolds *et al.* (1986b) reported that cluster exposure in the pre-véraison stage had no effect on the sugar concentration, but after véraison, the exposed treatments displayed higher levels. It is therefore important that the canopy is well exposed after véraison so that the clusters can receive enough sunlight to enhance sugar accumulation.

In hot regions, it was found that the sugar increased more rapidly than in cooler areas (Coombe, 1987b), but that too high cluster temperatures due to over-exposure inhibited sugar accumulation (Coombe, 1987b; Bergqvist *et al.*, 2001). It was further found that clusters that were too exposed to the sun, displayed a wider range of sugar levels without a change in the average, which meant uneven ripening (Coombe, 1987b).

Malic acid was found to be one of the most abundant solute in the flesh of unripe berries (Coombe, 1987a). According to Hunter *et al.* (1991a) and Hunter & Ruffner (2001) the highest total malic acid concentration was reached at pea size, while Gutiérrez-Granda & Morrison (1992) also found a high malic acid concentration prior to véraison.

The malic acid content declined during ripening by proportions comparable with the degree of increase that occurred in the glucose and fructose concentrations (Coombe, 1987a). From this, it could be derived that the metabolic breakdown products of malic acid was possibly used for the formation of sugars in the berry. It is however not that simple, as certain conditions, such as energy deficiency, must apply for the malic acid to be diverted from its normal metabolic pathway to form sugars. Iland & Coombe (1988), Hunter (1991), Hunter *et al.*, (1991a), Coombe (1992b) and Terrier *et al.* (1997) reported a decrease in malic acid from véraison to ripeness that could be explained by malic acid metabolism during ripening (Iland & Coombe, 1988). This process proved to be temperature dependent, as Coombe (1987b) found that malic acid metabolism was more rapid in hot viticulture regions.

Coombe (1987a) stated that the malic acid was lower in the vascular tissue than in other flesh segments because the respiration of malic acid was rapid in vascular bundles during ripening, and the consequent gradients led to malic acid movement towards these zones. The end result was uniform low malic acid levels in overripe grapes. According to Gutiérrez-Granda & Morrison (1992), the vascular tissue was the specific site of malate metabolism during ripening. Thus a gradient was maintained that resulted in malate diffusion toward the peripheral vascular tissue. As no clear correlation was found between the malic enzyme activity and the change in malic acid concentration in a specific tissue (Gutiérrez-Granda & Morrison, 1992), it was concluded that intracellular compartmentation, rather than enzyme availability, was responsible for the regulation of malate metabolism in grapes.

Possible additional malic acid reducing mechanisms were suggested by Hunter & Ruffner (2001), namely decreased malate formation due to inhibition of glycolytic carbon flow and re-metabolism of stored malic acid to satisfy a continuing demand for respiratory substrates. This re-metabolism may be favoured by compartmentation breakdown at the onset of the ripening period. According to the same source, Ruffner *et al.* (1975) stated that gluconeogenesis might also decrease the malate levels, particularly under low temperatures when respiratory rates, energy demands and sugar production were low.

Iland & Coombe (1988) also found that as the berries ripen, malic acid increased in the skin. Results of Gutiérrez-Granda & Morrison (1992) confirmed that. Although the malic acid in the skin was low prior to véraison, it started to increase in the week after that. It could probably be due to a migration of malic acid from the pulp to the skin. The highest malic acid concentration in the skin was found at ripeness.

An increase in the degree of shading was associated with higher juice malic acid content (Coombe, 1987b; Kliewer & Bledsoe, 1987; Archer, 1988; Smart *et al.*, 1988; Archer & Strauss, 1989a; Kliewer & Dokoozlian, 2000). According to Reynolds *et al.* (1986b) malic acid tended to be low in shaded treatments before véraison, and high in the same treatments after véraison. This could indicate that both malic acid accumulation and breakdown occurred slowly under these conditions. Bergqvist *et al.* (2001) also considered a decrease in malate metabolism to be the reason for the higher malate level found at ripeness in poorly exposed clusters.

Iland & Coombe (1988) found that **tartaric acid** accumulated in grape berries before véraison. According to Coombe (1987a), the highest concentration was found at 6 °B, while it decreased mainly between 6 °B and 10 °B to about one half of the original concentration. Hunter *et al.* (1991a) and Hunter & Ruffner

(2001) reported that the highest total concentration was reached at pea size. According to Iland & Coombe (1988), Hunter *et al.* (1991a), Coombe (1992b) and Gutiérrez-Granda & Morrison (1992), the tartaric acid content of grape berries changed very little from véraison to full ripeness. Coombe (1987a) reported a decline in tartaric acid concentration, which could be attributed to the dilution effect of berry growth (Rojas-Lara & Morrison, 1989). Gutiérrez-Granda & Morrison (1992), however, suggested that metabolism of tartaric acid occurred in the peripheral vascular bundles, as a decrease of tartaric acid in the outer mesocarp (the peripheral vascular tissue as well as the mesocarp parenchyma exterior to the vascular bundles) was noticed. In contrast, Iland & Coombe (1988) found no metabolism of tartaric acid in the berry during ripening. The small decrease in concentration they found in the flesh and skins was attributed to dilution due to berry enlargement during ripening. Iland & Coombe (1988) also reported an increase in the content of tartaric acid in the skin, which differed from the findings of Gutiérrez-Granda & Morrison (1992).

The tartaric acid content of the must decreased in unbalanced and too vigorous vines (Hunter, 1991) and with increasing canopy shade (Smart *et al.*, 1985b; Archer, 1988; Archer & Strauss, 1989a). According to Reynolds *et al.* (1986b), a higher tartaric acid occurred in exposed fruit post-véraison. Smart *et al.* (1988), however, found that an increasing degree of shading was associated with an increased juice tartaric acid concentration due to delayed ripening, while Calò *et al.* (1995) stated that the tartaric acid concentration was not very sensitive to the exposure of clusters to direct light.

According to Coombe (1987b), Smart *et al.* (1988), Archer & Strauss (1989a), Kliewer & Dokoozlian (2000) and Bergqvist *et al.* (2001), the **total acidity** tended to increase with shading. This higher acid concentration was due to the increased malic acid levels under shady conditions (Archer & Strauss, 1989a), which was probably the result of a lower rate of malic acid catabolism. It is in contrast with Smart *et al.* (1985b) and Archer (1988) who reported a lower

titratable acidity in shade conditions – according to the latter source due to lower tartaric acid contents. Reynolds *et al.* (1986b) reported a lower total acidity in shaded treatments before véraison, which could indicate less acid production in the berries, and higher levels after véraison compared to the sun exposed controls.

The acid content was noticeably reduced by higher temperatures (Calò *et al.*, 1995), probably due to the greater intensity of malic acid breakdown (Coombe, 1987b; Calò *et al.*, 1995). It was found that the tartaric acid remained more or less constant with an increase in temperature, while the pH increased due to an increase in potassium (Coombe, 1987b).

In practice, especially in regions with warmer climates favouring malic acid metabolism, it would be very important to create microclimatic conditions in die canopy during the pre-véraison stage that will favour sucrose production in the leaves and translocation to the clusters. This will guarantee high acid (particularly tartaric acid) in the berries so that the ripening period will be entered at high acid levels, favouring a lower berry pH at ripeness (Hunter & Ruffner, 2001).

Iland & Coombe (1988), Hunter (1991) and Gutiérrez-Granda & Morrison (1992) found an increase in **pH** after véraison with ripening. The ratio of salt to free acid forms of tartaric acid, plus the amount of free malic acid, determines the juice pH (Iland & Coombe, 1988). As some of the salt forms of tartaric acid do not contribute to acidity, there is no direct correlation between the titratable acidity and pH (Hunter, 1991). Gutiérrez-Granda & Morrison (1992) attributed the higher pH found in the skin compared to the fleshy tissue to the high potassium concentration in the former.

A negative correlation between the average light values in the canopy and the pH was generally found (Smart *et al.*, 1985b; Kliewer & Bledsoe, 1987; Archer, 1988;

Archer & Strauss, 1989a; Kliewer & Dokoozlian, 2000; Bergqvist *et al.*, 2001). A pH level above 3.6 in the wine may cause an increase in the relative activity of micro organisms such as bacteria, lower the colour intensity in red wines, bind more sulphur dioxide, and shorten the ability of the wine to age (Jackson & Lombard, 1993).

Potassium uptake was slow before véraison (Ollat & Gaudillère, 1995). Rogiers *et al.* (2000) also reported a slow potassium accumulation in berries during the pre-véraison phase, while Smart *et al.* (1985b) found an accumulation of potassium in the shoots between flowering and véraison. This slow potassium accumulation in the pre-véraison phase increased 3.5 times during the post-véraison berry enlargement phase (Rogiers *et al.*, 2000). The potassium content increased in all berry tissues after véraison with ripening (Conradie, 1981; Coombe, 1987a; Iland & Coombe, 1988; Coombe, 1992b; Gutiérrez-Granda & Morrison, 1992), with the most pronounced increase in the skin (Gutiérrez-Granda & Morrison, 1992). This increase could possibly be explained by the redistribution of potassium from the stems, leaves and petioles to the fruit during ripening (Smart *et al.*, 1985b), while Conradie (1981) found that the rate of potassium absorption by the vine decreased sharply between véraison and ripeness, despite the steady potassium increase in the clusters. This increased import of potassium into the berries occurred at the same time and in the same proportion as the increased sink strength of the berry and relative contribution of the phloem water flow (Ollat & Gaudillère, 1995). It was therefore concluded that most of the potassium was transported by the phloem sap.

Kliewer & Bledsoe (1987) found a negative correlation between the average light values and potassium. Potassium was also found to increase in unbalanced and vigorous vines with an increase in the level of shading (Archer, 1988; Archer & Strauss, 1989a; Hunter, 1991; Kliewer & Dokoozlian, 2000). Smart *et al.* (1985b) found that shade at véraison caused higher concentrations of potassium in the leaves, petioles, stems and rachises, which were subsequently associated with

higher must potassium levels. Whilst studying the effect of shading on grape composition, Rojas-Lara & Morrison (1989) found that the berries from the shaded treatment had a significantly higher potassium concentration than those from the exposed treatment.

According to Ollat & Gaudillère (1995), **calcium** accumulation in the berries occurred mainly in the pre-véraison stage when xylem water flow was high. After véraison it was found that the water import rate by phloem increased while xylem contribution decreased to almost zero (Ollat & Gaudillère, 1995). That explained why calcium accumulation almost stopped after véraison, as calcium was considered to be phloem immobile.

In contrast, Rogiers *et al.* (2000) found a linear accumulation of calcium throughout the entire developmental and ripening period of Shiraz. The more variable accumulation of calcium in comparison to that of potassium was explained by the fluctuation in xylem flow, which was more closely linked to variations in the soil-vine-atmosphere water potential gradients than would have been the case for phloem flow. It was therefore concluded that the xylem conduits remained functional during post-véraison enlargement of berries, although the increase in potassium:calcium ratio indicated that the relative contribution from phloem water flow increased post-véraison. So, according to Rogiers *et al.* (2000), either developing Shiraz berries are able to accumulate calcium (and potassium) via a non-vascular route, or the generalized model needs to be amended to accommodate the special case of the cultivar Shiraz. However, according to Hunter & Ruffner (2001), Düring *et al.* (1987) found that although the peripheral xylem vasculature was disrupted at véraison, the axial vessels remained largely intact. It was therefore considered possible that inflow through remaining xylem conduits (and possibly non-vascular apoplast) could continue during ripening.

According to Conradie (1981) **magnesium** only had one continuous absorption period in the vine, contrary to nitrogen, phosphate, potassium and calcium. During the growth season, the clusters received about 15 percent of the total magnesium absorbed by the vine. Magnesium uptake in the berries was slow before véraison (Ollat & Gaudillère, 1995) and increased afterwards, although to a lesser extent than potassium. It was further found that magnesium was translocated to the berry both by xylem and phloem conduits. Smart *et al.* (1988) stated that an increase in the degree of canopy shading was associated with a non-significant increase in juice magnesium concentration.

The vine apparently has two distinct periods during which **nitrogen** absorption takes place. The first period starts off slowly after bud break, accelerating subsequently to reach a maximum between the start of bloom and véraison. The second peak period starts after harvest, and absorption continues at a relatively slow rate up to the end of leaf fall (Conradie, 1980). According to Ollat & Gaudillère (1995) nitrogen uptake in the clusters was slow before véraison and increased afterwards. As nitrogen uptake by the vine ceased between véraison and harvest, the increased levels in the clusters seemed to have been supplied mainly by the roots and leaves (Conradie, 1980) *via* both the xylem and phloem conduits (Ollat & Gaudillère, 1995).

Vigorous growth and resultant shading were generally associated with higher nitrogen content in the clusters (Hunter, 1991). A significant increase in juice ammonium-nitrogen (NH_4-N) concentration under these circumstances was also found, while the nitrate-nitrogen (NO_3-N) and total nitrogen increased non-significantly. This increase was probably due to the inhibiting effect of shading on nitrate reductase activity in the leaves, and thus on the nitrogen metabolism in the vine (Smart *et al.*, 1988).

The accumulation of precursors for **anthocyanin** synthesis was favoured at véraison (Hunter & Visser, 1988a), which explains why Hunter *et al.* (1991b)

found the highest anthocyanin content in the berries 20 to 30 days after véraison. There was a decline in total anthocyanin content of berries during the later stages of ripening (Hunter *et al.*, 1991b; Haselgrove *et al.,* 2000).

The berry skin colour was related to at least three factors operating separately (Iacono *et al.*, 1994), namely berry sugar, cluster exposure and crop load (leaf area/fruit mass ratio). According to Haselgrove *et al.* (2000) anthocyanin metabolism responded to changes in both light and temperature. Kliewer (1970) found that lower (20°C) day temperatures significantly increased the level of anthocyanin pigments in the skins at both high and low light intensities, while low light intensity greatly reduced the colouration of Pinot noir grapes at both high (30°C) and low (20°C) day temperatures. It was also found by Haselgrove *et al.* (2000) that the anthocyanin levels per berry increased up to a ripeness level of 22 °B and then decreased with further berry ripening. The effect of light and temperature on anthocyanin production was relatively greater than on sugar accumulation (Kliewer, 1970). Johnstone (1996) found a strong relationship between the soluble solids and the colour in Shiraz, while a more precise study done by Hunter *et al.* (1991b) showed a closer positive correlation between the sugar levels in the berry skins and the anthocyanin concentration.

Environmental factors that favoured the accumulation of carbohydrates in plant tissues have been generally associated with enhanced anthocyanin synthesis in grapes (Kliewer, 1970). On the other hand, Wicks & Kliewer (1983) found that the anthocyanin level changed without any significant change in skin carbohydrate (according to Hunter *et al.*, 1991b). Kliewer (1977) found that high nitrogen levels in the soil led to lower anthocyanin levels due to increased protein and amino acid synthesis and storage.

Light was found to be the limiting factor in anthocyanin accumulation, especially during the early stages of ripening (Haselgrove *et al.*, 2000), although the colour responses to light intensity differed between different cultivars (Kliewer, 1970). It

was generally found that light exposure led to higher anthocyanin concentrations, while shaded conditions tended to result in a low colouration (Archer, 1988; Smart *et al.*, 1988; Calò *et al.*, 1995; Keller & Hrazdina, 1996; Haselgrove *et al.*, 2000; Kliewer & Dokoozlian, 2000; Tomasi *et al.*, 2000; Bergqvist *et al.*, 2001). More detailed studies showed that the skins of berries in shaded canopies had lower colour density and total and ionised anthocyanin (Smart, 1982; Smart *et al.*, 1985b). Smart (1982) found that wine produced from grapes that had developed in the shade was low in colour density and had a poor colour hue as rated by a panel of oenologists.

The formation of colour in the berry skin decreased in unbalanced and too vigorous vines. A decrease in both the total anthocyanins and the colour density was found (Hunter, 1991). According to Hunter *et al.* (1991b), Roubelakis-Angelakis & Kliewer (1986) stated that sunlight proved to be indispensable for phenylalanine ammonia lyase activity. Phenylalanine ammonia lyase (PAL) was found to be the key enzyme in the shikimic acid pathway that channelled phenylalanine away from protein synthesis towards that of flavanoid and anthocyanin synthesis.

Too high temperatures during early berry ripening inhibited anthocyanin synthesis and/or increased anthocyanin breakdown (Haselgrove *et al.*, 2000), since the optimal temperature for anthocyanin synthesis was between 17°C and 26°C. Coombe (1987b) and Bergqvist *et al.* (2001) found an increase in anthocyanins with an increase in temperature, but only up to a certain point, whereafter a decrease in anthocyanins with a further increase in temperature occurred. It is therefore important to have a canopy where the clusters receive sufficient light for anthocyanin synthesis, but are protected from excessive berry heating – especially for vines grown in hot viticulture areas.

According to Johnstone (1996), the main elements that affected the **phenolic compounds** (thus including the flavour components) were the genetic properties

of the vines, the environment (climate, soil and topography of the site), the design of the vineyard and cultivation practices such as irrigation, fertilizer input, and crop and canopy manipulation. The latter two are considered important, as Calò *et al.* (1995) reported that the precursors of aroma components were synthesized in the leaves, while the synthesis and evolution of the components themselves occurred in the grape berries. Phenolic compounds seemed to be mainly accumulated in the berry skin (Bravdo & Naor, 1995; Calò *et al.*, 1995). In the case of seeded cultivars, it was found that 10 percent of the total phenols of the berry were present in the juice, 30 percent in the skin and 60 percent in the seeds (Boulton *et al.*, 1998). For wine making purposes the phenol content of the seeds is not considered to be very important. Phenolic compounds are, next to carbohydrates, the most abundant in plants (Hunter, 2001). In grapes, the phenol content of the must could be crucial to quality by affecting the colour, astringency, tannin character and ageing potential of red wine (Hunter, 1991).

The total phenol concentration increased for a short while during the early ripening process, whereafter it decreased steadily (Kataoka *et al.*, 1983). However, it was found by Singleton (1966) that the total phenols per berry increased until rather late in the maturation stage, which indicated that the continued synthesis of phenolic compounds was slower than the rate of berry enlargement.

According to Johnstone (1996), perhaps the most readily apparent effect on flavour over which the producer may have some control, is the harvest date. Research is being done on optimal ripeness for certain cultivars which will enable the producer to harvest when the grape phenol content is at an optimum for quality wine production. It may even be that maximum aroma will be attained before all the sugar has accumulated in the berries, as Calò *et al.* (1995) found that metoxypyrazine levels decreased markedly after véraison during maturation, while Marais (1992) reported decreased carotenoid levels with berry ripening. High temperatures during the ripening stage could explain this observation, as

phenols tended to have a similar reaction pattern as anthocyanins to temperature changes (Coombe, 1987b).

An excessive cluster temperature thus has a negative effect on the flavour profile, while the amount of sunlight exposure of the clusters also plays a prominent role – in cooler climates even more so. Jackson & Lombard (1993) found that although volatile terpenes increased slowly in a cool site, the concentrations at ripeness tended to be high. Some compounds, like metoxypyrazines, were even at undesirably high levels. According to Marais (1992) higher carotenoid levels were found with grapes produced in hotter areas than with those produced in cooler regions. Also, in warmer viticulture regions a greater possibility for the development of undesired unripe, herbaceous characters in the berries was found as the level of shading in the canopy increased (Haselgrove *et al.*, 2000). Lower phenol content was also found under vigorous growth conditions where the canopy had a shaded interior (Smart *et al.*, 1985b; Coombe, 1987b; Smart *et al.*, 1988; Hunter, 1991). However, according to Marais (1992), the carotenoid levels were consistently higher in grapes exposed to shade or low light intensities compared to grapes exposed to direct sunlight or high light intensity. The better sunlight exposure due to canopy management changed the flavour profile and enhanced the typical flavour of the cultivar (Volschenk & Hunter, 2001), which resulted in higher complexity in the wine (Hunter & Fouché, 2000).

Sunlight exposure of the clusters increased the levels of phenolic compounds, monoterpenes (Hunter & Fouché, 2000; Kliewer & Dokoozlian, 2000) and quercitin and decreased the methoxypyrazine (Kliewer & Dokoozlian, 2000) and carotenoid levels (Marais, 1992). Razungles *et al.* (1996), however, found that berries exposed to sunlight before véraison were richer in carotenoids, while cluster exposure after véraison favoured the conversion of these pigments to norisoprenoids. Calò *et al.* (1995) also found that accumulation of

norisoprenoids was favoured by direct exposure of clusters to sunlight, since light exposure stimulated the catabolism of carotenoids to form isoprenoids.

It is thus important for the canopy to be well exposed before véraison to enhance the accumulation of various flavour compounds. After véraison the clusters should receive diffused sunlight – enough for the conversion of carotenoids to norisoprenoids, but not enough to increase the cluster temperature excessively.

2.2 GRAPE YIELD AND QUALITY

The magnitude of a commercial harvest seems to depend on the proportion of assimilates partitioned towards cluster development rather than vegetative growth (Kriedemann, 1977). According to Hunter & Visser (1990b), vegetative dominance should be minimized without reducing assimilate supply to the fruit so that the required balance between vegetative and reproductive growth is still maintained. Photosynthesis is particularly important in relation to the total yield and the distribution of assimilates to the different plant parts (Calò *et al.*, 1995) - thus improved radiation (intensity and duration) will lead to an increase in yield. Canopy management of shaded vineyards may simultaneously increase grape yield and wine quality - as it was found that all yield components were affected by shade (Smart *et al.*, 1990).

According to Archer (1988) and Hunter (1991) low light intensities decreased the budding percentage and fertility of basal buds, which explains the lower yield found by Smart *et al.* (1989). Archer & Strauss (1989a) found that the buds needed a minimum light intensity of 30 $\mu E.m^{-2}.s^{-1}$ to remain fertile, while Hunter & Visser (1990b) managed to increase bud fruitfulness by exposing the basal buds to higher light intensities and by changing the source:sink relationship. May & Antcliff (1963) also observed that the fruitfulness and consequently the yields were severely depressed in the season following a shading treatment.

Apart from altering the light regime of the bud, shading affected its temperature. It might well be that a reduced import of assimilates into the bud (when shaded) contributed to the reduced fruitfulness. This decrease did not seem to be related to the light quality, but rather to a reduction in total light intensity (May, 1965) that affected the nutrient and export status of the whole plant.

Keller & Hrazdina (1996) found that the yield was primarily determined by nitrogen availability during bloom, as low nitrogen supply reduced fruit set due to inflorescence necrosis. May *et al.* (1973) stated, according to Kriedemann (1977), that fruit set, rather than leaf exposure, was a primary limitation to yield in the grapevine. According to Caspari & Lang (1996) the carbohydrate supply was the major determinant of fruit set. Symptoms similar to early bunch stem necrosis (EBSN) increased as the carbohydrate supply decreased, suggesting that this disorder could sometimes be caused by low carbohydrate supply. Jackson (1991), according to Caspari & Lang (1996), found that EBSN was increased (and fruit set decreased) by shading, reductions in leaf area and water and nutrient supply – all of these factors reduced the carbohydrate availability.

The effect of shade on fruit set is little studied (Smart *et al.*, 1990), but poor fruit set in the centre of dense canopies is commonly observed. According to Archer & Strauss (1989a) low light intensities had a negative effect on berry set. Smart & Smith (1988) found that canopy shade of vigorous vines caused reduced bud break, fruitfulness and, due to reduced berry set, decreased bunch mass (Smart *et al.*, 1989).

May & Antcliff (1963) stated that bunch mass under shady conditions was reduced because of smaller, and possibly fewer, berries. According to Rojas-Lara & Morrison (1989) vines with shaded foliage had smaller berries than exposed vines. Archer & Strauss (1989a) also reported a reduction in berry mass, cluster mass and yield per vine due to the effect of shading, while

according to Reynolds *et al.* (1986a), increased cluster exposure led to a higher berry mass.

On the other hand, Kliewer & Antcliff (1970) and Haselgrove *et al.* (2000) found that the mass of the shaded berries was significantly higher than that of the exposed berries, while Bergqvist *et al.* (2001) concluded that the smaller mass of exposed berries may have resulted from the effects of elevated berry temperature on berry cell division or elongation as well as increased fruit transpiration rates and subsequent berry dehydration. It therefore seems as if shading of the leaves has a different effect on berry size than cluster shading, since the former resulted in smaller berries, while the latter induced the development of larger berries with a higher mass. Still, it was clear that maintenance of enough and efficient leaf area to nourish the rapidly dividing cells of young berries was critical for obtaining high yield at harvest (Hunter & Visser, 1990b).

According to Bidan (1977), it had frequently been shown that the best red wines were obtained from grape varieties with small berries, as the most important factors contributing to the originality and quality of wines were localized in the skin. McCarthy (1996) also mentioned the general recognition that smaller berries tended to result in more highly coloured and flavoursome wines, but stated that this translated into lower yield. Bravdo & Naor (1995) found that small berries had a better potential for enriching the must, while Hunter (1991) stated that smaller berries due to cultivation practices had a higher skin:pulp ratio that resulted in an increase in wine quality. Small berries had a higher surface area to volume ratio than larger berries and produced a more intense wine (Trought, 1996), whereas, according to Gray *et al.* (1997), larger berries tended to have lower anthocyanin and phenol concentrations. According to Boulton *et al.* (1998) the berry size could be kept small (and the quality therefore increased) by special management such as early water stress, although he stated that this is very difficult to accomplish under certain circumstances. It should, however, be kept

in mind that water deficit during the stage of rapid berry cell division will result in a smaller yield (Van Zyl, 1981). A compromise should thus be made between the negative effect on yield quantity and the positive effect of a smaller berry on yield quality.

Grape quality depended mainly on the interaction between climate (link between temperature, solar radiation and water) and genotype (Calò *et al.*, 1995). The elements of climate that could have affected quality were the temperature, rainfall or irrigation, light intensity and cloud cover, wind and the mesoclimate (Jackson & Lombard, 1993). Soils may also have an effect on grape quality – either directly by nutrition, or indirectly by regulating the quantity of plant available water. Therefore, it is important that the soil conditions (physical, chemical and biological) enhance root development and distribution. A well-developed root system will increase the buffer capacity of the root system and will have an effect on grape quality due to better utilization of the available soil volume.

The balance between yield and vegetative growth seemed useful to explain variation in wine quality (Scienza *et al.*, 1995). In the quality defining process, relationships between yield and vegetative growth must accordingly be implemented with the description of the interaction between the environment and the variety/clone (plant nutrition, soil and/or site effect), which may determine changes in wine quality due to different ripening processes. According to Scienza *et al.* (1995), Mescalchin *et al.* (1995) stated that the must quality was related to the source:sink ratio that was, in turn, linked to the environment. Smart (1984) was of the opinion that microclimate, water and nutrient supply were the most important factors affecting wine quality in the vineyard. The microclimate should not be restrictive, while water and nutrient supply should be somewhat less than optimal. According to Escalona *et al.* (2000), the quality seemed to be higher when the water supply was sub-optimal for vegetative growth. The mechanism by which irrigation management affected grape composition was mainly indirect by nature, due to the effect on growth vigour and the size of the

yield (Van Zyl, 1981). In practice it is therefore necessary to ensure that the nutritional status of the grapevine is adequate but not excessive in order to attain not only optimum production, but also better wine quality (Conradie & Saayman, 1989).

According to Hunter (1991) yield, must and wine composition were negatively affected by too vigorous growth. The consequent decrease of sunlight and temperature in the canopy did not only have an effect on the berry size, but also on the metabolic activity of the cluster. As a lower grape value index (indication of grape quality) was found for leafy, dense canopies with poor fruit exposure (Gray *et al.*, 1997), it could be concluded that vine vigour, as well as the concomitant shading, affected grape maturation, composition and thus the eventual quality of the must and wine (Hunter, 1991).

Canopy shade of vigorous vines was associated with delayed grape maturation (Archer, 1988; Smart *et al.*, 1988; Smart *et al.*, 1989; Keller & Hrazdina, 1996), while Rojas-Lara & Morrison (1989) found that shaded canopies led to delayed berry growth and ripening. Optimum ripening also seemed to be inhibited (Archer, 1988). According to Archer & Strauss (1989a) the negative effect of excessive vegetative growth on canopy microclimate was clearly mirrored in the poor qualitative and quantitative performance of the vine, while Keller & Hrazdina (1996) underlined the importance of the microclimate for obtaining optimum quality grapes by stating that fruit quality was primarily determined by light intensity during véraison. Jackson & Lombard (1993) linked excessive shading to unbalanced must that resulted in poor wine quality. Smart *et al.* (1989) also found that a shaded canopy microclimate was unfavourable to wine quality, while Haselgrove *et al.* (2000) stated that the wine character (including cultivar character) and quality were modified by altered light conditions. According to Smart (1982) shading in canopies was a significant factor in reducing red wine quality in hot areas, as wines made from grapes that matured in shaded canopies had low quality scores.

The degree of cluster exposure also affects grape quality, since Reynolds *et al.* (1986a) found that increased cluster exposure improved the fruit composition. The composition of grapes and thus, the level of maturation, was according to Valenti *et al.* (1995) not only due to the photosynthetic activity of the leaves, but also to the quantity of light that reached each individual cluster during maturation. However, it was found that berry temperature increased with incident radiation (PAR). Although higher temperatures would normally enhance berry growth and ripening (Jackson & Lombard, 1993), there seemed to be an upper limit above which assimilation of quality compounds was reduced. Caution is necessary in drawing conclusions about the role of temperature *per se* in determining the composition and quality of wine grapes, as correlations with other climatic factors may be equally valid (Coombe, 1992a). Both the direct (light quantity and quality) and the indirect (temperature mediated) effects of sunlight exposure influenced the berry composition. Especially in warm climates it was found that prolonged fruit exposure to direct sunlight should be avoided (Bergqvist *et al.*, 2001).

Apart from berry growth, it seems as if shaded leaves also have a different effect on berry composition than shaded clusters. According to Kliewer & Antcliff (1970) and Rojas-Lara & Morrison (1989), leaf shading delayed and reduced the rate of berry growth and sugar accumulation. Kliewer & Antcliff (1970) found that covered clusters had heavier berries with higher total soluble solids than the exposed clusters, while Rojas-Lara & Morrison (1989) found no significant differences. According to Rojas-Lara & Morrison (1989) leaf shading had a larger effect on the potassium and malate content of the berries (and thus the pH) than cluster shading, while Kliewer & Antcliff (1970) found that the total acidity of the covered clusters were significantly higher than that of the exposed clusters. Cluster shading affected anthocyanin accumulation significantly, while leaf shading had little effect in this regard (Rojas-Lara & Morrison, 1989). It is therefore important to describe any shade treatments used during research.

High vegetative growth is also counterproductive to desirable grape production and quality due to strong competition by the growing shoot tips for newly produced carbohydrates (Boulton *et al.*, 1998). On the other hand, too high yield (thus over-cropping) may also decrease grape and wine quality (Jackson & Lombard, 1993). In such a case, the photosynthetic capacity of the vine will be unable to ripen all the clusters. If the vines are over-cropped, the harvest date will either be significantly delayed or the grapes will never reach the desired maturity levels. Low sugar content is the primary signal for over-cropping, while the delayed harvest date will lead to wines with inadequate acidity in warmer climates. Although the retained acid may be adequate under cooler conditions, the wine will still be unbalanced due to an imbalance in grape composition. The grape aroma and other constituents appearing late in ripening are also likely to be deficient (Boulton *et al.*, 1998). Bravdo *et al.* (1985) found that cluster thinning may be used to increase the quality, but this has a limit (Boulton *et al.*, 1998). There seemed to exist a threshold value for crop load below which no increase in quality is observed. It is therefore essential that a balanced grapevine, with a sufficient and efficient leaf area to fully ripen the grapes, be created.

3. CANOPY MANAGEMENT TO OBTAIN HOMOGENEOUS GROWTH

3.1 CANOPY STRUCTURE AND THE IDEAL CANOPY

According to Carbonneau (1995) the microclimate, total photosynthesis, yield, berry maturation, as well as the wine quality, were dependent on the canopy structure. The surface area was shown to be correlated with must and wine analysis, while the leaf area (LA):trellis surface area (SA) ratio, which is an indication of the canopy density, correlated very well with must and wine analyses and sensory scores (Smart, 1982). The LA:SA ratio was significantly correlated with microclimate. The latter could be an indicator for physiological

function affecting fruit composition and ultimate wine quality (Smart *et al.*, 1985a).

Archer & Strauss (1989a) also found that the canopy microclimate was dependent on the amount and spatial distribution of the leaf surface. The exposed leaf area that was able to reach photosynthetic potential, and thus ensured a largely positive carbon balance for the plant beyond its own carbon requirement, was a good estimation of the physiological potential of the canopy (Carbonneau *et al.*, 1997).

3.2 AIM OF CANOPY MANAGEMENT

According to Hunter & Visser (1990a), canopy management should be aimed at creating a canopy consisting of well-positioned leaves, favouring the maximum interception of sunlight as well as maximum photosynthetic activity, without reducing the quantity and quality of the grapes. In accordance to that, Kliewer & Dokoozlian (2000) stated that canopy management refers to the arrangement of shoots and clusters for optimising exposure to sunlight and to facilitate air movement in the fruiting region with the objectives of maximizing canopy light exposure, vine productivity and wine quality.

Volschenk & Hunter (2001) investigated the effect of canopy management on Chenin blanc vines, in relation to no canopy management. The control vines (where absolutely no short-term canopy management practices, including shoot positioning, were carried out) resulted in a relatively high level of light penetration into the cluster zone, mainly from directly above the cordon. The canopy centre and some of the clusters were therefore overly exposed, whereas a high percentage of the leaves and clusters were too shaded. The canopy management vines had a more uniform interception of sunlight throughout the whole canopy due to the more efficient accommodation of shoots, which led to a more homogeneous ripening of all the clusters.

According to Boulton *et al.* (1998) it is important for clusters to be exposed to light and air, without direct overhead sunlight, which will increase the risk of sunburn. Clusters buried within the canopy, however, often fail to ripen properly. Canopy management is therefore aimed to improve the microclimate and to balance the vegetative:reproductive growth (Hunter, 1991) so that carbon allocation to fruit sinks can be optimised without disturbance to growth and development in other parts of the grapevine (Hunter, 2000).

Smart *et al.* (1990) stated and justified five canopy management principles that are important to the producer to obtain quantity, quality and longevity from vineyards.

- A large canopy surface area well exposed to sunlight is desirable, and this surface area should develop as quickly as possible in spring.
- Canopies should not be so close together as to cause excessive shade at the base of adjacent canopies. Vertical canopies are preferred and the ratio of canopy height to row width should not exceed about 1:1.
- Canopy shade should be avoided, especially in the cluster/renewal zone. Leaves and fruit should have as uniform a microclimate as possible.
- Photosynthetate partitioning between shoot and fruit growth should be appropriate to avoid either excess or deficient leaf area relative to the fruit mass. The number of actively growing shoot tips should be limited during berry ripening.
- Arranging locations of individual organs in restricted zones in space facilitates mechanisation, i.e. of shoot tips for trimming, of cane bases for winter pruning and of fruit for mechanical harvesting. Training system design should as much as possible create fruiting/renewal zones at a similar height for any one vine.

3.3 SOURCE:SINK RELATIONSHIPS IN GRAPEVINES

It is important for the producer to understand certain balances that exist within the vine in order to make informed decisions regarding canopy management practices.

According to Hunter (1991) it is very important to maintain the balances between vegetative and reproductive growth, and reserve accumulation. It was found that physiological processes and the ultimate wine quality decreased in the cases of unbalanced vegetative and reproductive growth. Scienza *et al.* (1995) found this balance (between yield and vegetative growth) to be useful to explain variation in wine quality. As Mescalchin *et al.* (1995) (according to Scienza *et al.*, 1995) stated that must quality was related to the source:sink ratio, the assumption can be made that manipulation of the source:sink ratio may lead to a better balance between vegetative and reproductive growth.

A source:sink relationship expresses a biochemical exchange between a producing organ and a consuming organ (Carbonneau, 1995).

A possible definition of a sink could be a receiver of assimilates (Ho, 1988). The sink strength expressed the ability to import assimilates, which could be measured as an absolute growth rate or net accumulation rate of dry matter. The import rate was regulated by the metabolic activity of the sink organ during development, and could be altered by changing the sink strength or the strength of competing sinks.

It was found that yield could be changed by altering the priority in assimilate partitioning. Altering the potential reproductive sink strength of an individual sink could have this result. The controlling step(s) in the regulation of the partitioning of dry matter into different organs seemed to be the metabolic processes inside the sink cells, which also primarily controlled the import of assimilate. The actual sink strength was thus largely determined by factors that affected rate-limiting

processes within the sinks during development. Therefore, optimisation of the rate-limiting processes by manipulating growth conditions could be an effective way to increase the crop yield. The quality of products could also be improved by manipulation of compartmentation and metabolism of the imported sugars in sinks (Ho, 1988).

Sink organs were divided into two groups, namely utilization sinks, where most of the imported assimilate were used for growth, and storage sinks, where substantial amounts of imported assimilate were stored (Ho, 1988). According to Hunter *et al.* (1994), the partitioning of assimilates between sites of production, utilization and accumulation primarily determined the yield and longevity of grapevines.

Source limitation of net photosynthesis occurred when the yielding capacity of the reactions that supplied assimilates were inadequate for the demand of the sink tissues (Iacono *et al.*, 1995). In the grapevine it could be seen as over-cropping, with a high reproductive to vegetative growth ratio (mostly human-induced) (Bravdo & Naor, 1995). Over-cropping resulted in insufficient assimilate supply to the clusters, delayed maturation, poor colouration and low aroma and flavour.

Baysdorfer & Bassham (1985) stated (according to Iacono *et al.*, 1995) that sink limitation to net photosynthesis occurred when the rate at which assimilates were utilised and stored was less than that at which it was supplied to the sink tissues. Under-cropping resulted in excessive vegetative growth and delayed maturation due to an increase in assimilate flow to the shoot growing tips rather than to the clusters (mostly human-induced) (Bravdo & Naor, 1995). In the case of low vigour, Arfelli *et al.* (1995) showed that cluster thinning (decreased reproductive:vegetative growth ratio) could led to an increase in the sugar content of the remaining clusters. These results indicated the existing balance between reproductive and vegetative growth. Cluster thinning is generally only

recommended when vines experience, or is expected to experience, stress conditions.

Over-cropping and under-cropping are examples of vines that are not in balance. According to Archer (1988), a vine is in balance when active shoot growth stops just after véraison. Otherwise the sink strength of the growing shoots would be stronger than that of the maturing clusters, and an optimum ripeness level would not be reached. An appropriate leaf surface:fruit ratio on the vine may ensure a satisfactory ripening of good and rather high yields, without a decrease in the quality of the fruit and the resulting wines, as long as over-cropping is avoided (Safran, 1977). Higher yields and quality are achieved by the successful regulation of source:sink relationships in the production and utilisation of assimilate within a plant (Ho, 1988). This must be achieved under field conditions.

3.4 DIRECTION OF TRANSLOCATION DURING THE GROWTH SEASON

Because of leaf age differences, the import:export ratio in the canopies of field grown vines continuously change during the growth season (Hunter *et al.*, 1994), meaning that, depending on the time during the growth season, different leaves are sources and different organs may act as sinks. Therefore, the different leaf age groups play a major role in the continuous changing of the import:export kinetics in the canopy as the growth season progresses (Hunter & Le Roux, 1997).

An important factor in the translocation pathway of nutrients is the leaf canopy itself (De la Harpe, 1983). Changes in the leaf area or exposition to the sun will affect the rate of photosynthesis, which will in turn affect the translocation of photosynthetate.

As already discussed, young primary leaves were sinks for photosynthetic products and only started to act as sources when they have reached 50 percent of their final size (Kriedemann *et al.*, 1970).

During the **initial growth stage of the shoot**, it was found that the first assimilate exported by a leaf was directed towards the shoot tip. Only when that leaf was separated from the shoot tip by two or three other exporting leaves, did some of the assimilate get transported to the permanent vine structure (Hale & Weaver, 1962). Quinlan & Weaver (1970) stated similar findings.

According to Koblet (1977), the most basal leaf on a young, growing shoot exported most of its carbohydrates basipetally. Until the **flowering** stage, the translocation from the leaves in the middle portion of the shoot was found to be bi-directional, while the apical leaves mainly exported assimilate to the shoot tip. It could therefore be stated that the growing shoot tip and the parent material were more powerful sinks than the flower cluster, as the young inflorescence was unable to influence the direction of translocation (Hale & Weaver, 1962). The import of assimilate to the inflorescence was only improved after the demand by the developing leaves have been met (Ho, 1988).

Koblet (1977) found that all shoots exported their products partially to adjacent shoots, while Hunter & Ruffner (2001) also found evidence that indicated the likeliness that the clusters imported sucrose from the adjacent shoot(s) as well as from the rest of the vine structure. During flowering, Quinlan & Weaver (1970) found that no movement of assimilate occurred between adjacent shoots arising from the same spur, while movement of photosynthetic products from shoots into the parent material was minimal.

The shoot tips and parent vines may have been more powerful sinks than the clusters during flower development, but not during **berry set** (Hale & Weaver,

1962). According to Hunter (1991) the cluster was the strongest sink for assimilate in the stage after flowering and berry set.

At berry set, distribution from the apical leaves was very restricted, probably because they had not yet reached export maturity. The leaves positioned in the middle part of the shoot translocated acropetally to the growing shoot tip and apical leaves, as well as basipetally to the clusters. The basal leaves mainly fed the clusters (Hunter & Visser, 1988a).

When fruit development started, leaves below the cluster translocated both to the cluster and the parent vine (Hale & Weaver, 1962). Quinlan & Weaver (1970) also reported the competition between the cluster and the parent vine for assimilates at berry set.

Quinlan & Weaver (1970) further found that the removal of the shoot tip and cluster resulted in the translocation of assimilates to an adjacent shoot. This observation indicated the importance of these two sink organs in the determination of the pattern of photosynthetate translocation.

At **pea size**, it was found that the apical, middle and basal leaves translocated to the clusters (Hunter & Visser, 1988a). Haselgrove *et al.* (2000) also found that after véraison, when the rate of shoot elongation decreased sharply, assimilates were translocated from the shoot tips in a basipetal direction. As berry ripening proceeded further, it was found that the predominant movement of photosynthetate from apical leaves was mainly basipetally to the berries (Koblet, 1977). De la Harpe (1983) found a multidirectional movement of assimilates in the shoots, rather than only a basipetal movement, independent of the position of the leaves on the shoot.

At **ripeness**, assimilate for growth and development of the clusters were mainly obtained from the leaves in the cluster zone (Hunter & Visser, 1988a), while

almost no export of assimilate was found from the basal leaves ("below" the clusters) at the end of ripening (Koblet, 1977). De la Harpe (1983) found that at ripeness, in contrast to the export of photosynthetates at véraison, a very slow rate of translocation took place and that even the organs concerned with storage did not constitute a very strong sink at that time. Hunter & Ruffner (2001) also stated that the sink strength of the berry seemed to have decreased at the end of the ripening period. According to Hunter & Visser (1988a), the translocation of assimilates towards vegetative organs was resumed at ripeness, possibly to supplement the accumulation of reserves as well as the regrowth of the shoot tips.

According to Hale & Weaver (1962) secondary shoots acted as sinks until one or two of their leaves reached maturity, whereafter they were self sufficient as no assimilates moved into them from the primary shoot. It was actually found by Koblet (1977) that secondary shoots without clusters exported their carbohydrates to the clusters on the primary shoot, while it did not seem to happen where the secondary shoots were fertile. In contrast with Hale & Weaver, De la Harpe (1983) found that assimilates are imported by secondary shoots from the primary shoot throughout berry ripening. It is therefore clear that, although the netto direction of translocation remains the most important, translocation should not be seen as only one directional, but rather as an interchange between the different vegetative parts of the vine. It was found that the yield as well as the total contents of individual sugars in the berries at ripeness was decreased by secondary shoot removal, which indicated that secondary shoots in the canopy have a more important function than realized and that they do make a contribution to grape development and composition (Hunter, 2000).

The demand for photosynthetate by sinks fluctuated enormously, but had a downward trend as the season advanced (Kriedemann, 1977). The findings of De la Harpe (1983) indicated that translocation in the vine had virtually stopped

at ripeness. Along with this diminishing requirement, individual leaves achieved lower and lower photosynthetic rates towards the end of the growth season. It could possibly be explained (according to Hunter & Visser, 1988a) by the increased total canopy leaf area (increased source); senescence of the leaves; or decreased vegetative and reproductive growth (decreased sink demand).

Quinlan & Weaver (1970) found that a reduction in the level of available assimilates within a shoot, or part of a shoot, caused a compensatory movement of photosynthetates from adjacent leaves. This movement was possible either within a single shoot or between different shoots. The opposite was also found to be true – removal of a sink increased the availability of assimilates to adjacent sinks.

The statement could therefore be made that any changes in the relative activity, or sink capacity, of the different growth centres may affect the pattern of assimilate distribution in the phloem system of the vine. Hunter & Le Roux (1997) also found that growth compensation, resulting from alteration of the canopy due to canopy management practices, directly affected the assimilate distribution dynamics.

3.5 LONG-TERM PRACTICES

Although canopy practices are normally associated with treatments that are executed during the growth season, it must be kept in mind that long-term cultivation decisions have a large effect on the canopy structure and density in a specific growth season.

The importance of young vine training was stressed by Zeeman & Archer (1981) and Archer (personal communication). Uniformity of young vine training with upright stems, even spacing of the spurs and cordons of equal length, led to an even distribution of the leaves, shoots and clusters (Zeeman & Archer, 1981),

with the resultant better aeration and drying off after irrigation/rain, lowered risk of fungal diseases, and an easier harvesting process. Stems that were not upright, led to unbalanced cordon lengths and therefore unbalanced shoot growth (Archer, 2001). Homogeneous shoot vigour is important in order to obtain a high yield of evenly ripened clusters.

According to Jackson & Lombard (1993), the level of light interception, shoot density and the microclimate could be modified by the trellis design. An even distribution of shoots led to the optimum use of available sunlight energy for photosynthesis (Zeeman & Archer, 1981), while a satisfactory microclimate could only be obtained, according to Smart (1984), with low shoot number per vine. It is important to have the shoots as closely spaced as possible (depending on the growth) to promote the yield, but not so close as to cause shaded conditions which reduce fruit quality and/or bud fruitfulness (Smart, 1988). Canopy quality could also be regulated by the thoroughness of application of the winter pruning system (Zeeman & Archer, 1981).

Other long-term canopy management practices include soil preparation, choice of rootstock-scion combination, vine spacing, as well as fertilization and irrigation programs (Hunter, 1991). The last two could also be defined as short-term practices and, according to Archer (1988) and Boulton *et al.* (1998), the adaptation of the irrigation and fertilization programs were in many cases enough to control vegetative growth. Boulton *et al.* (1998) also mentioned the trellising system to be an important factor to cope with excessive vigour, while Smart (1992) suggested systems with large canopy surface areas for sites with high vigour potential. The trellising system is therefore an important means to improve the canopy microclimate as well as yield and quality.

3.6 SHORT-TERM PRACTICES

Many studies have been done around short-term canopy management practices, with the emphasis on the way, timing and extent of the specific action to alter source:sink relationships to the benefit of grape yield and composition as well as grapevine longevity. Such practices included suckering, shoot positioning, shoot tip removal (topping and tipping) and the removal of leaves in the cluster zone and above (Archer, 1988; Hunter, 1991; Hunter 2000).

3.7 VINEYARD HETEROGENEITY

According to Smart (1988) large heterogeneity of shoot growth exists in standard vines. The shoot length distribution was found to be bimodal, where lengths of 20 cm to 40 cm and 80 cm to 100 cm were the two most frequent classes.

A large proportion of underdeveloped shoots were found in shaded canopy interiors. These shoots often grew to less than 40 cm in length with less than ten nodes. The shorter shoots had smaller leaves, fewer secondary leaves, shorter internodes, and a lower leaf area:shoot length ratio than normally developed shoots (Smart, 1988). According to Archer (2001), shorter shoots also tended to develop in the middle of longer cordons.

Peterson & Smart (1975) mentioned that short shoots may have insufficient leaf area to adequately ripen their fruit, while research quoted by Long (1987) showed the fruit flavour and concentration to be optimum when there was a proper relationship between active leaves and crop on a shoot-to-shoot basis. In order to ripen their clusters, Koblet (1977) found that short shoots imported more assimilate from adjacent shoots than did normally developed shoots. Grapes from the shorter shoots showed nevertheless a slight reduction in sugar concentration as well as a reduction in colour and phenols. Research quoted by Long (1987) showed that wine made from those grapes had low levels of ethanol, colour and phenol compounds. The assumption could thus be made

that the presence of short shoots could be responsible for a decrease in the grape quality of the other, stronger shoots from the same vine and in this way affect the quality of the total crop.

Long shoots represented the diversion of photosynthetate into a superfluous leaf area, which in turn contributed to canopy shading (Smart *et al.*, 1990), while optimum ripeness of the clusters could not be attained (Archer, 2001). Long shoots were mostly found at the end of cordon arms and close to the split of the cordon.

While comparing two different vineyards, Long (1987) found that the vineyard that consistently produced better flavoured wine had less variability in ripeness. In accordance, Smart *et al.* (1990) stated that high quality wines probably resulted from processing fruit of relatively similar composition. Fruit composition in a vineyard is usually described as a mean value (Trought, 1996), although the variation around the mean may have an important impact on fruit quality. Even among clusters on the same vine and among berries within a cluster there is always a degree of variability in berry composition and stage of development (Rojas-Lara & Morrison, 1989). Where the variation around the mean is large, the potential for the presence of overripe and unripe flavours in the must and wine is increased, even though the average composition may seem acceptable (Long, 1987; Trought, 1996).

Apart from the effects of sunlight exposure (Coombe, 1987b), asynchronous ripening may be enhanced by the varying leaf area:fruit ratio of individual shoots (Jackson & Lombard, 1993). Equality in shoot growth seems important for the production of homogeneous, top quality grapes (Archer, 2001).

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CHAPTER 3

RESEARCH RESULTS

THE EFFECT OF SHOOT HETEROGENEITY ON VEGETATIVE GROWTH PARAMETERS OF SHIRAZ/RICHTER 99 GRAPEVINES

1. ABSTRACT

In this study vegetative growth parameters of normally and underdeveloped shoots were compared in an attempt to quantify shoot heterogeneity in a Shiraz/Richter 99 vineyard. The field trial was performed in the Stellenbosch area, Western Cape, South Africa. Comparisons based on certain vegetative growth parameters were made between normally and underdeveloped shoots from shaded and well-exposed canopies. The longer primary shoots of the normally developed shoots matured earlier in the season with less apparent competition between shoot lignification and grape ripening. Reserves were more evenly distributed in these shoots. Total starch content over the whole shoot was found to be higher in the normally developed shoots, particularly when well exposed. More and longer secondary shoots occurred on the normally developed shoots than on the underdeveloped shoots. No difference was found in the number of primary leaves (leaves on primary shoots) between normally and underdeveloped shoots, although the leaf area was much larger in the case of the former. Normally developed shoots had more and larger secondary leaves (leaves on secondary shoots), while all the leaves that developed in the shaded canopies were found to be larger than those in the well-exposed canopies with a higher leaf area:mass ratio. The normally developed shoots seemed to have a greater potential for producing a higher yield with better quality than the underdeveloped shoots, as they have a more desirable leaf area composition in addition to the larger total leaf area per shoot.

2. INTRODUCTION

Wine industries all over the world are committed to produce grape and wine quality suited to meet the challenges of ever-increasing national and international market competition and requirements (Hunter & Archer, 2001a). This often requires an increase in grape and wine quality without a decrease in the yield or longevity of the vine. Carbon allocation to the clusters should therefore be optimised without detrimentally affecting the growth and development of other parts of the vine (Hunter, 2000). A skilful and comprehensive management

strategy, which includes long and short-term cultivation practices, is needed (Hunter & Archer, 2001a).

According to Carbonneau (1995) the yield, berry maturation and wine quality are dependent on the canopy structure, as it defines the microclimate and thus the photosynthetic activity and carbon output of the canopy. Well-positioned shoots, leaves and clusters that are optimally exposed to maximize sunlight interception and photosynthesis are essential to obtain a canopy in which each individual leaf contributes to the photosynthetic capacity of the vine (Archer, 1988; Hunter & Visser, 1990a; Kliewer & Dokoozlian, 2000).

The size and quality of a commercial harvest seem to depend on the proportion of assimilates partitioned towards cluster development rather than vegetative growth (Kriedemann, 1977). According to Hunter (1991) it is very important to maintain the balances between vegetative growth, reproductive growth and reserve accumulation, as it was found that physiological processes and the ultimate wine quality decreased in the case of unbalanced vines.

This balance is also important on a shoot-to-shoot basis. According to Archer (2001) the quality of each individual cluster is directly proportional to the physiological output of its shoot. Long (1987) mentioned that flavour and concentration are optimum when there is a proper relationship between the active leaves and the clusters per individual shoot. It is accepted that 10 cm^2 to 12 cm^2 leaf area is generally required to ripen one gram of fruit (Hunter & Visser, 1990b, and references therein). Short shoots may therefore have insufficient leaf area to adequately ripen their clusters (Peterson & Smart, 1975), which may lead to increased import of assimilates from adjacent shoots and the rest of the permanent vine structure (Koblet, 1977) and a decrease in overall quality of the yield.

In an attempt to quantify shoot heterogeneity in a Shiraz/Richter 99 vineyard, certain vegetative growth parameters of normally and underdeveloped shoots were measured.

3. MATERIALS AND METHODS

Experimental vineyard

A seven year old *Vitis vinifera* L. cv. Shiraz, clone SH1A, grafted onto Richter 99 (*Vitis Berlandieri* x *Vitis rupestris*), clone RY2A, vineyard was used for this study. The vineyard is situated at the experimental farm of the Agricultural Research Council (ARC) Infruitec-Nietvoorbij near Stellenbosch in the Western Cape (Mediterranean climate). The vines are spaced 2.75 m × 1.5 m on a Glenrosa soil with a western aspect (26° slope) and trained onto a 7-wire lengthened Perold trellising system with movable canopy wires (VSP). Rows were orientated in a North-South direction.

Micro sprinkler irrigation was applied at pea size berry and at véraison. Pest and disease control was applied during the growth season according to the standard program of the ARC.

Experiment design

The experiment was laid out as a completely randomised 2×4×2 factorial design. The three factors were: degree of canopy exposure (well-exposed and shaded canopies); ripening stages (one, three, four and five weeks after véraison); and level of shoot development (normally and underdeveloped shoots). There were three replications for each of the 16 treatment combinations.

Shaded canopies were only shoot positioned and topped, whereas additional suckering and leaf thinning were applied in order to create well-exposed canopies. Selection of underdeveloped shoots was based on length and comparative lack of lignification at véraison (Fig. 1).

Measurements

Vegetative parameters: a total of five normally developed shoots from fifteen randomly selected vines were used for each treatment at each ripening stage. Ten underdeveloped shoots under the same conditions were used, to ensure a large enough berry sample to perform all the necessary analyses. Primary and secondary shoot length (cm) and mass (g), degree of lignification of primary shoots, number of primary and secondary leaves per shoot, leaf area (cm^2) and leaf mass (g) of primary and secondary leaves, as well as the starch content

(mg/g dry mass) of the basal, middle and apical parts of the main shoots were measured.

The degree of lignification of the shoots was scored from one to five – five being completely lignified and one still completely green. The leaf area was measured with a LICOR LI-3100 area meter (Lincoln, Nebraska, USA).

Shoots sampled at five weeks after véraison were divided into three parts, namely basal, middle and apical, whereafter only the internodes were analysed for starch. Both the nodes and the internodes were used for the determination of the fresh and dry mass of the shoots. Calculation of the total starch content per shoot was based on the assumption that the starch content of the nodes was the same as that of the internodes. The internodes were frozen at –20°C prior to freeze-drying with a Chriss Alpha freeze-drying unit. The shoots were then ground and milled with a Tecator Cyclotec 1093 Sample mill.

Extraction of sucrose, hexoses and organic acids: [Described by Hunter *et al.* (1995b)].
Dry material (0.5 g) was suspended in 25 mL methanol-chloroform-formic acid [MeOH – $CHCl_3$ – 0.2 M HCOOH (12:5:3 v/v)] and homogenized for 30 seconds using a Janke & Kunkel Ultra-Turrax T25 macerator, which operated at 20 500 rpm. The homogenate was transferred to a 0.45 μm filter and extraction of the residue repeated with 25 mL 80% ethanol. The residue was freeze-dried and kept for starch analysis.

Extraction and analysis of starch: [Described by Hunter *et al.* (1995a)].
A 50 mg freeze-dried residue sample was weighed into an Eppendorf tube, 1 mL 80% aqueous acetone added, and the suspension vortexed for 10 seconds and sonicated for 10 min. The suspension was left at 4°C for 6h, centrifuged (in the Eppendorf) and the supernatant decanted. Then 1 mL ethanol was added to the residue, the suspension vortexed for 10 seconds, sonicated for 10 min, centrifuged and the supernatant decanted. After addition of 1 mL water, the ethanol-procedure was repeated and the residue freeze-dried overnight. Water (550 μL) was then added to the lyophilised material, the suspension vortexed (10 seconds) and sonicated (10 min). The sample was then left at 4°C for an hour and centrifuged (10 min). By following this procedure, all sucrose, hexoses and organic acids were removed.

The sample was then heated in a boiling water bath (5 min with open caps and 60 min closed) to induce gelatinisation of starch. After cooling, 500 μL of an enzyme mix containing 5 U α-amylase (Sigma A-6380) and 2 U amyloglucosidase (Sigma A-7255) in 0.1 M Na-acetate (acetic acid/Na-acetate) buffer (pH 5.0) was added, the mixture vortexed for 10 seconds and incubated at 40°C under constant shaking (35 rpm) to hydrolyse starch (vials were vortexed for 10 seconds every 30 min). After 3h the samples were centrifuged (10 min) and diluted (1:29) with water.

Glucose generated from starch was determined by using the ABTS [2,2' azino-di(3 ethylbenzthiazoline)-6'-sulphonate] reagent, which consisted of 3.45 g $Na_2HPO_4.2H_2O$, 1.6 g $NaH_2PO_4.H_2O$, 2350 U glucose oxidase (Boehringer no. 646423), 375 U peroxidase (Boehringer no. 127361) and 125 mg ABTS (Boehringer no. 102946) dissolved in 250 mL water.

A 50 μL aliquot of the diluted sample was mixed with 950 μL of the above reagent. Absorbance was read at 420 nm after 30 min, with a LKB Biochrom Ultrospec spectrophotometer (II E) using 2 mm quartz cells. The blank consisted of a mixture of water and reagent. To obtain a glucose standard curve, seven standards of 0, 5, 10, 20, 30, 40 and 50 mg glucose/100 mL, were prepared. Results are expressed in mg starch per gram dry mass after multiplication with a factor of 0.9, which allows for the reduced molecular weight of glucose in the polymer.

Light intensity measurements: the photosynthetic photon flux density ($W.m^{-2}$) was measured in the vineyard with an ADC portable photosynthesis meter (The Analytical Development Co., England). The apparatus consists of an infra-red CO_2 analyser, a data logger, a Parkinson broad leaf chamber and air supply unit. Volume of the chamber is 16 cm^3 and the area 6.25 cm^2. The length of the air supply tube is 4 m. Radiation was measured using a quantum line sensor with filters providing response from 400 nm to 700 nm. The maximum vapour pressure (E_{max}) was taken as two, while the air flow rate through the open system was adjusted to 300 $cm^3.min^{-1}$ (Hunter & Visser, 1988b). Measurements were taken at 10:00 on the day scheduled (31 January, 8 February and 21 February 2002). Sun leaves in the basal (first three leaves above the bunches) position on the shoot were measured in all cases, whereafter the measurements obtained were converted to molar units per square metre per second ($\mu mol.m^{-2}.s^{-1}$). Three leaves per replicate were measured.

Statistical analyses

For statistical analyses, a factorial ANOVA was used. A 5% level of significance was applied. Depending on the data, non-parametric bootstrap analyses were used. Differences were considered significant when no overlapping of the 95% confidence intervals occurred.

4. RESULTS

Primary shoot growth

The normally developed primary shoots were significantly longer than the underdeveloped shoots ($p \leq 0.01$) – an average length of 112 cm compared to 50 cm. The canopy treatment did not have an effect on the primary shoot growth of the underdeveloped shoots, while the normally developed shoots from the exposed vines were somewhat shorter than those from the shaded vines (Fig. 2).

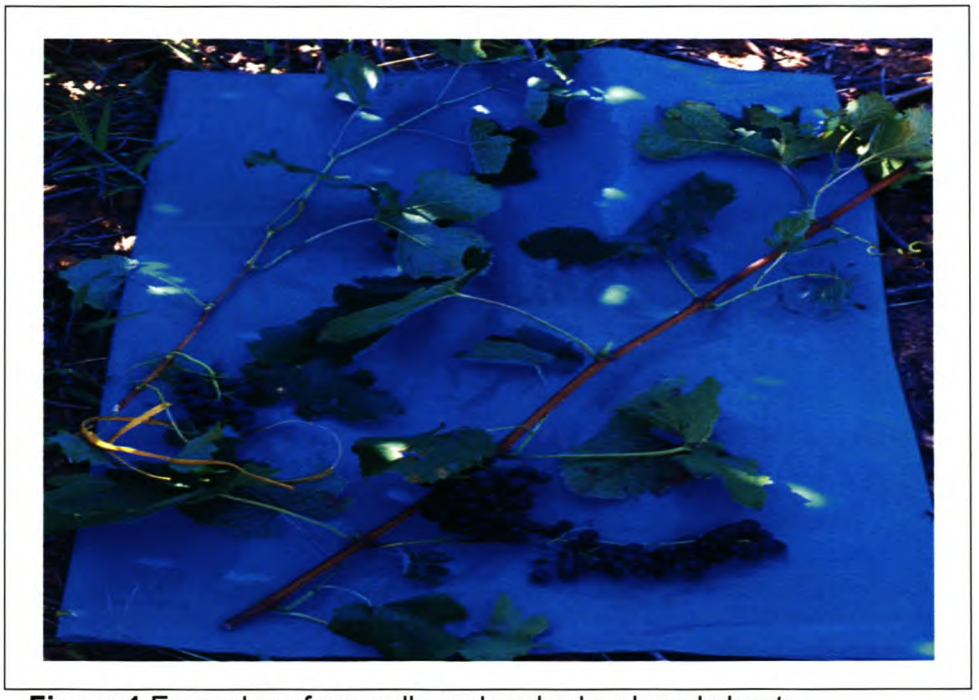

Figure 1 Examples of normally and underdeveloped shoots.

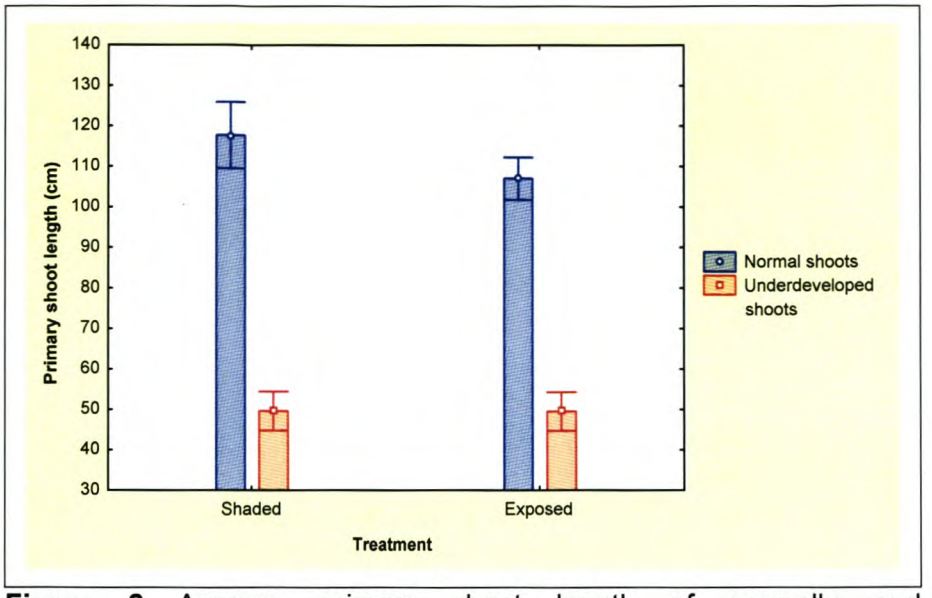

Figure 2 Average primary shoot length of normally and underdeveloped shoots in shaded and well-exposed canopies. Error bars indicate 95% confidence intervals.

Although the primary shoot length did not increase after véraison (data not shown), the mass of especially the normally developed shoots peaked at four weeks after véraison, whereafter it decreased. Underdeveloped shoots showed a similar pattern, but far less pronounced ($p \leq 0.05$) (Fig. 3). Shoot mass of normally and underdeveloped shoots tended to be higher in well-exposed compared to shaded canopies (data not shown).

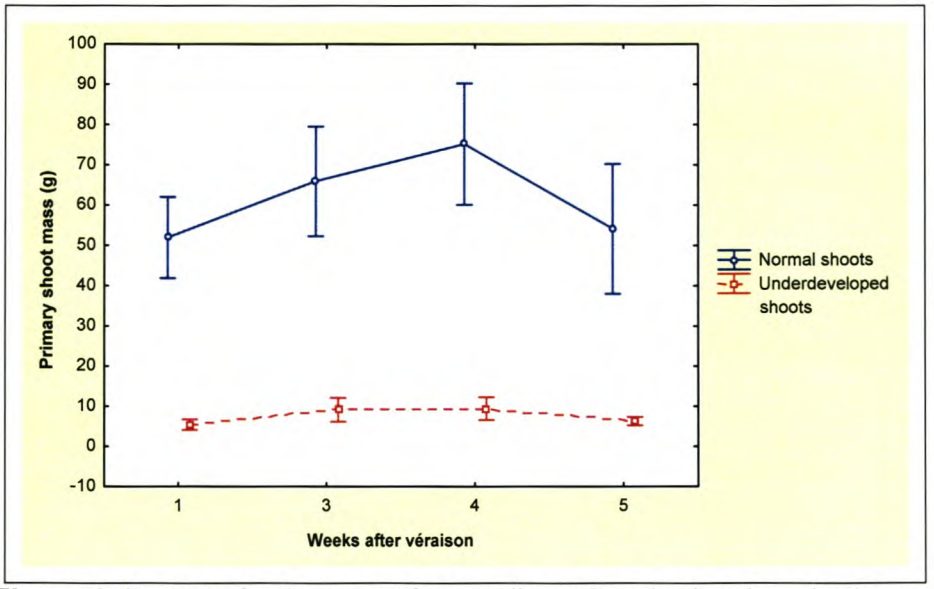

Figure 3 Average fresh mass of normally and underdeveloped primary shoots at one, three, four and five weeks after véraison. Error bars indicate 95% confidence intervals.

Secondary shoot growth

Significantly more and longer secondary shoots developed on normal shoots compared to underdeveloped shoots ($p \leq 0.01$). In the case of underdeveloped shoots, there seemed to be a non-significant increase in the number of secondary shoots in the well-exposed vines (Fig. 4). Longer and heavier secondary shoots were found on normally developed shoots in well-exposed canopies compared to shaded canopies, while the secondary shoots of underdeveloped shoots in shaded canopies had a longer average length (albeit larger variation) with no difference in mass (data not shown).

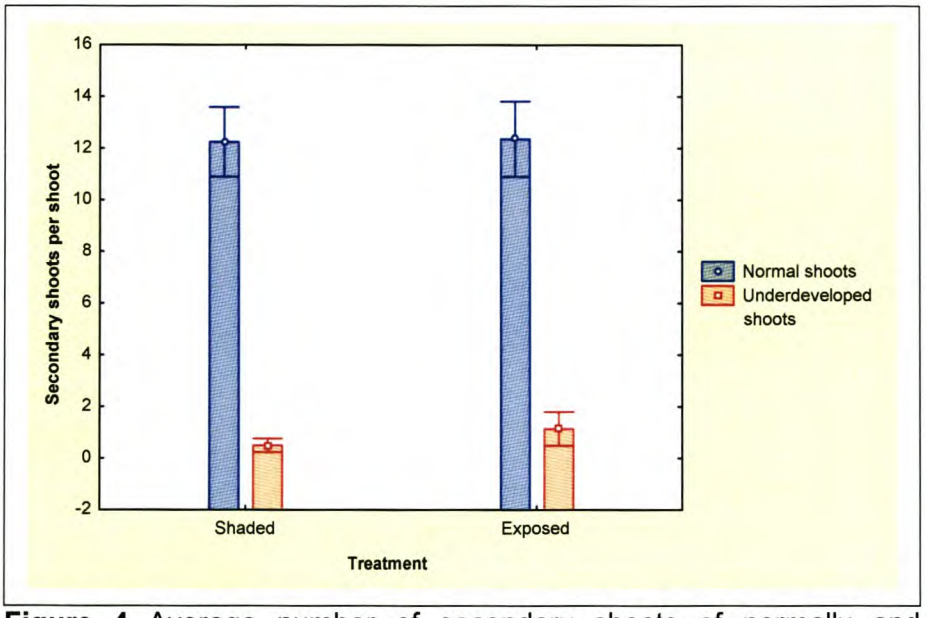

Figure 4 Average number of secondary shoots of normally and underdeveloped primary shoots in shaded and well-exposed canopies. Error bars indicate 95% confidence intervals.

Lignification

It was found that lignification of the normally developed shoots was far more advanced at véraison than that of underdeveloped shoots ($p \leq 0.01$); it was therefore used as a criterion for shoot classification. The degree of lignification tended to be higher in the well-exposed canopies (data not shown). This is in accordance with Reynolds *et al.* (1986) who found that periderm formation seemed to be a function of shoot density, as a higher percentage of poorly ripened shoots occurred in shady canopies. In the five weeks after véraison, the shoots became more lignified, the underdeveloped shoots to a larger extent than the normally developed shoots ($p \leq 0.05$) (Fig. 5).

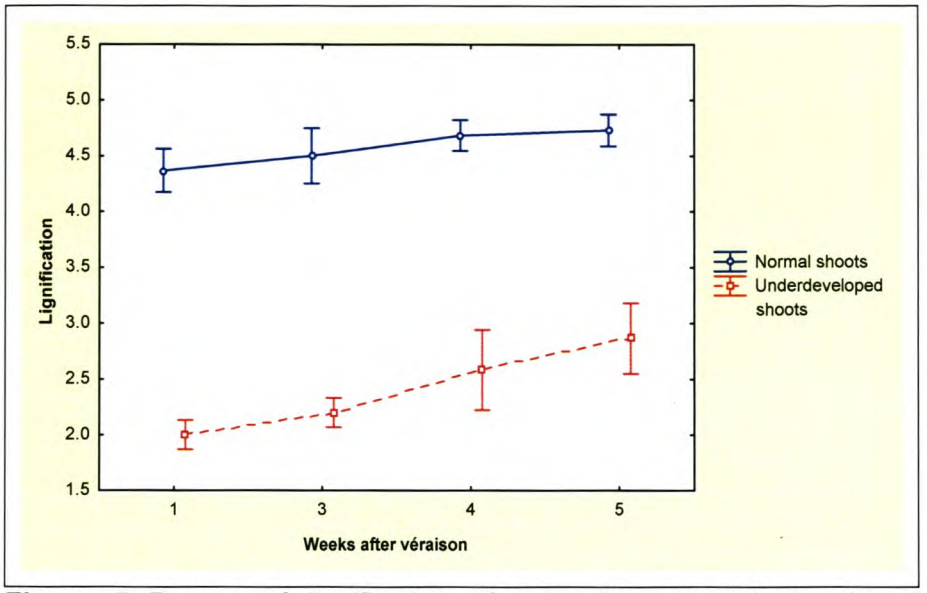

Figure 5 Degree of lignification of normally and underdeveloped primary shoots at different ripening stages after véraison. Different ripening stages indicate the number of weeks after véraison. Error bars indicate 95% confidence intervals.

Starch content

The starch that accumulated in the normally developed shoots (expressed as mg/g dry shoot mass) seemed to be more equally distributed over the length of the shoot (Fig. 6), with no significant difference between the canopy treatments (data not shown). Starch content (grams per shoot of part of the shoot) in both the normally and underdeveloped shoots tended to decrease from the basal to the apical part of the shoot (Fig. 7). This decrease was much more pronounced (percentage wise) in the underdeveloped shoots.

Although not statistically significant (data not shown) the degree of canopy exposure did play a role in the accumulation of starch in the shoots as all of the normally developed shoots situated in well-exposed canopies had a higher total starch content than those in shaded canopies.

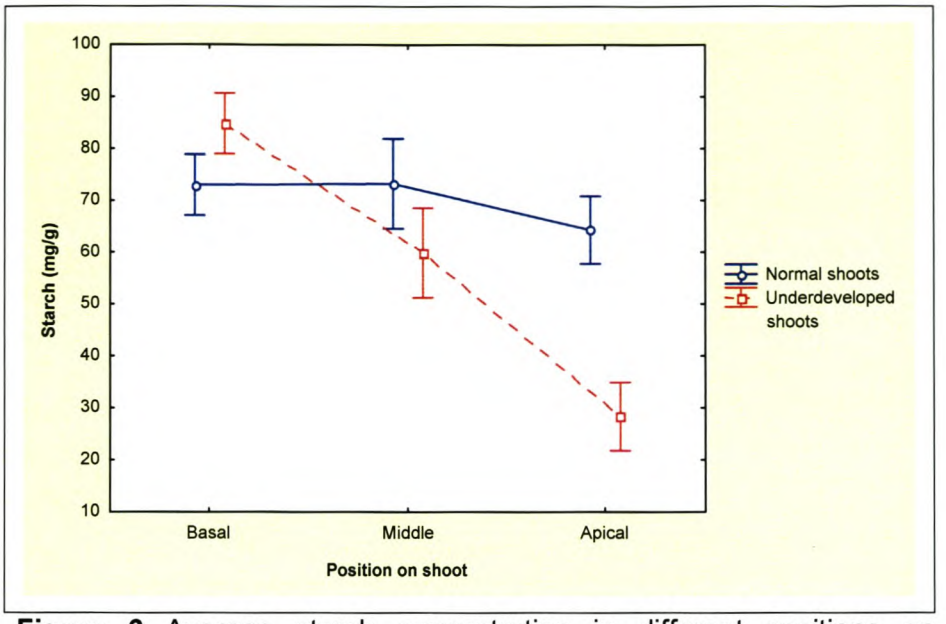

Figure 6 Average starch concentration in different positions on normally and underdeveloped shoots. Error bars indicate 95% confidence intervals.

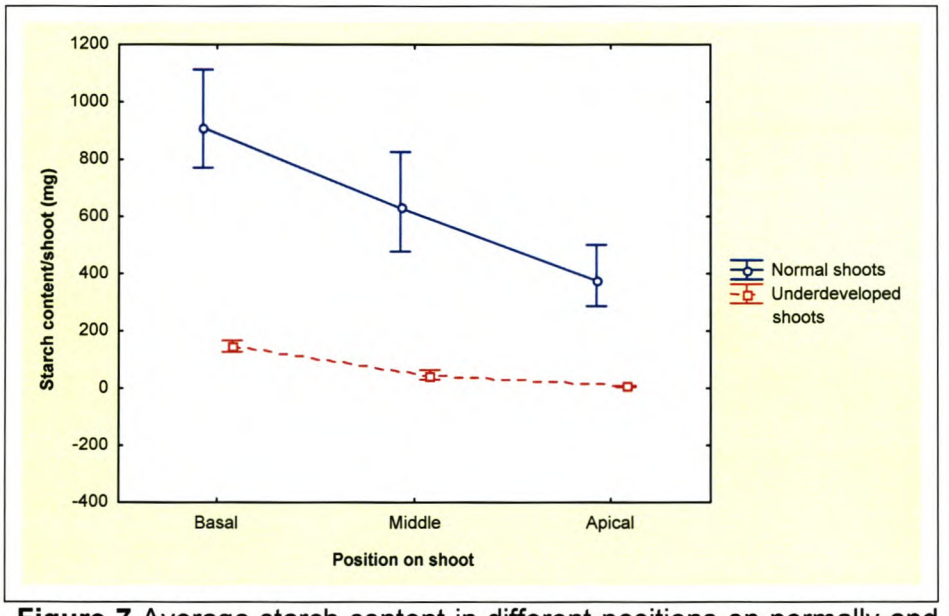

Figure 7 Average starch content in different positions on normally and underdeveloped shoots. Error bars indicate 95% confidence intervals.

Number of primary leaves

No statistically significant difference was found between the number of primary leaves per shoot on normally and underdeveloped shoots. The normal shoots from the shaded canopies tended to have more primary leaves than those from

the well-exposed canopies (albeit not significant), whereas no difference was found in the case of underdeveloped shoots (Fig. 8).

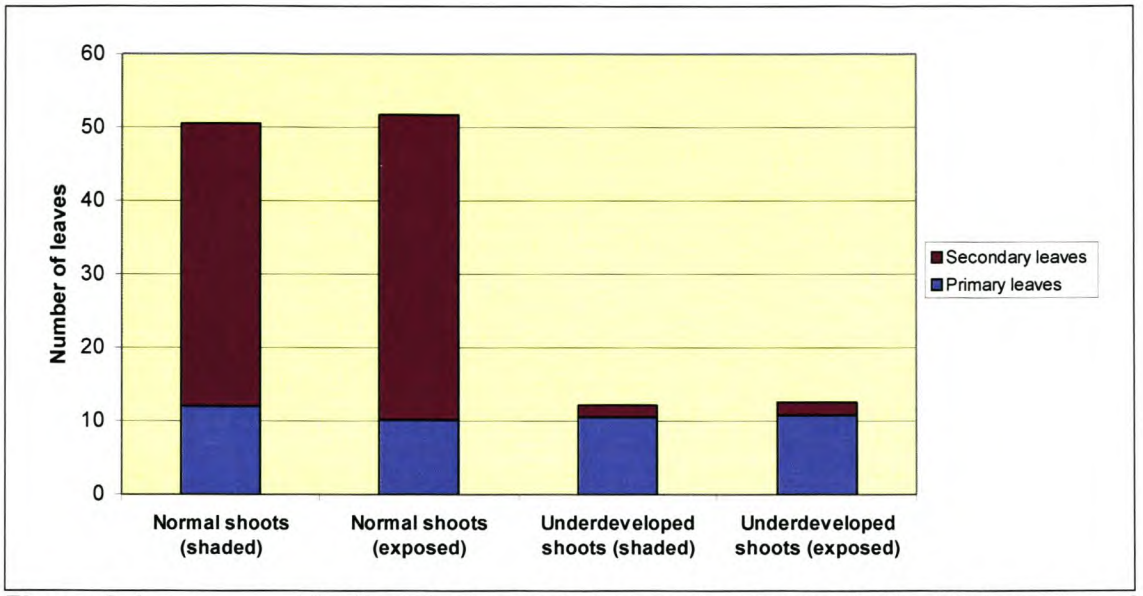

Figure 8 Average contribution of primary and secondary leaves to the total number of leaves per shoot.

Primary leaf area

Significantly larger primary leaves were found on normally developed shoots compared to underdeveloped shoots ($p \leq 0.01$) (Fig. 10).

The primary leaves of the normally developed shoots in the shaded canopies seemed to make a larger contribution to the total leaf area per shoot than in the exposed canopies (Fig. 9). Except for the higher number of primary leaves per shoot in the shaded canopies (Fig. 8), the leaves were also somewhat larger than in the exposed canopies (Fig. 10).

The same was found with the underdeveloped shoots, namely that the primary leaves that developed in the shade had a larger area (Fig. 10). Therefore, as no significant difference in the number of primary leaves was found (Fig. 8), the primary leaves of the underdeveloped shoots in the shaded canopies tended to make a larger contribution to the total leaf area per shoot than in the exposed canopies (Fig. 9).

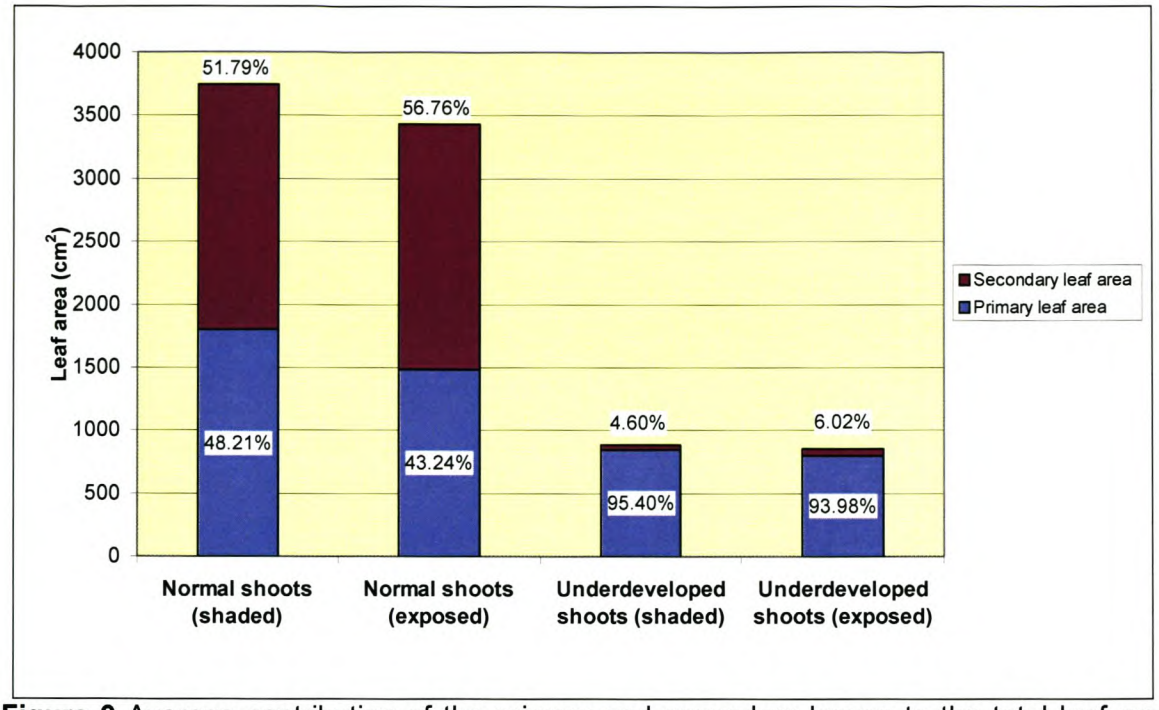

Figure 9 Average contribution of the primary and secondary leaves to the total leaf area per shoot.

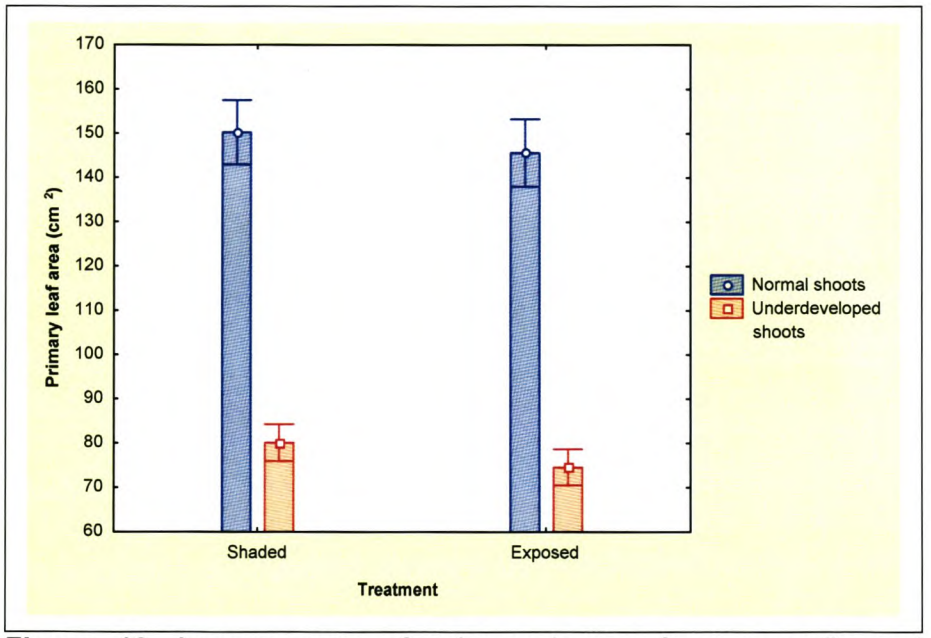

Figure 10 Average area of primary leaves from normally and underdeveloped shoots in shaded and well-exposed canopies. Error bars indicate 95% confidence intervals.

Number of secondary leaves

Significantly more secondary leaves were found on normally compared to underdeveloped shoots ($p \leq 0.01$). The canopy treatment also played a larger role in the case of the normally developed shoots, as more secondary leaves were found on the shoots in well-exposed canopies, whereas no differences were evident on underdeveloped shoots between the canopy treatments (Fig. 8).

Secondary leaf area

Significant larger secondary leaves were found on the normally developed shoots compared to the underdeveloped shoots ($p \leq 0.01$) (Fig. 11).

Regardless of the canopy treatment, the secondary leaves made similar contributions to the total leaf area on normally developed shoots (Fig. 9). Although more secondary leaves per shoot were found for the exposed vines (Fig. 8), the leaves had a larger mean area in the shaded canopies (Fig. 11).

Secondary leaves on the underdeveloped shoots in the well-exposed canopies tended to have somewhat larger mean area than in the shaded canopies (Fig. 11). It was, however, not statistically significant and did not make any difference in the composition of the total leaf area per underdeveloped shoot (Fig. 9).

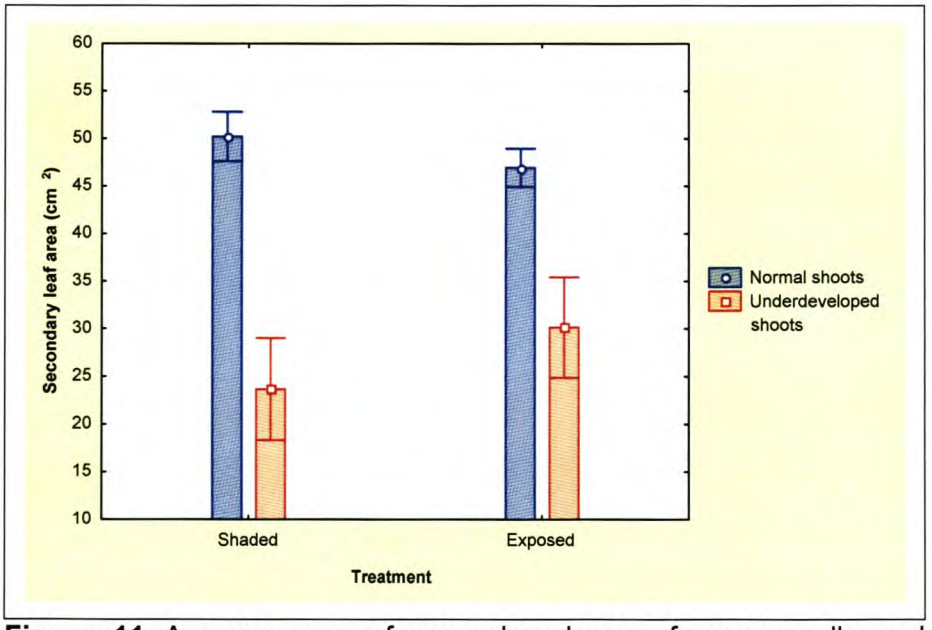

Figure 11 Average area of secondary leaves from normally and underdeveloped shoots in shaded and well-exposed canopies. Error bars indicate 95% confidence intervals.

Leaf area:leaf mass ratio

Primary (data not shown) as well as secondary leaves (Fig. 12) on the normally developed shoots had a significant lower leaf area:leaf mass ratio than the underdeveloped shoots ($p \leq 0.01$). All leaves in well-exposed canopies tended to have a lower ratio than in shaded canopies, the difference for the secondary leaves being more evident.

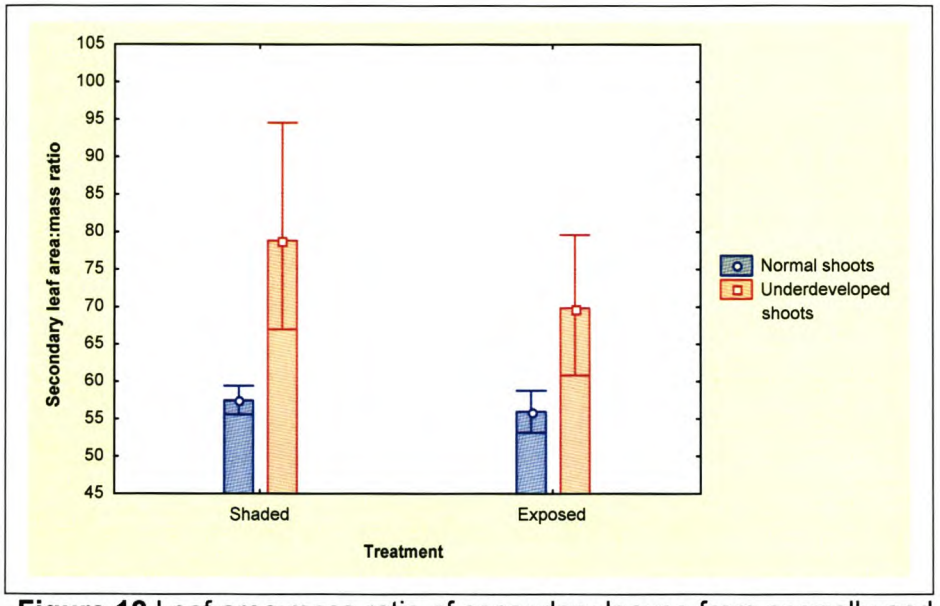

Figure 12 Leaf area:mass ratio of secondary leaves from normally and underdeveloped shoots in shaded and well-exposed canopies. Error bars indicate 95% confidence intervals (bootstrap analysis).

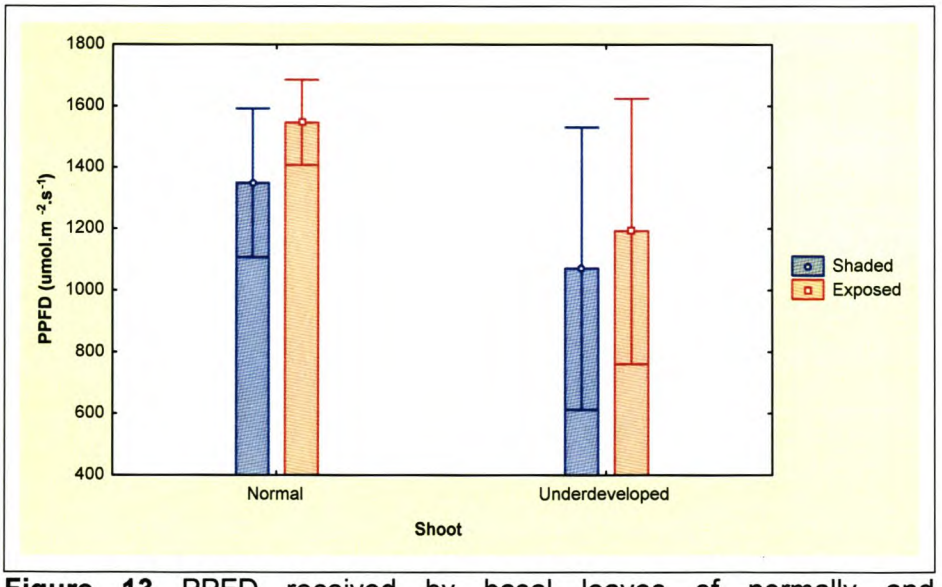

Figure 13 PPFD received by basal leaves of normally and underdeveloped shoots in shaded and well-exposed canopies. Error bars indicate 95% confidence intervals.

5. DISCUSSION

Primary and secondary shoot growth

The normally developed primary shoots in the shaded canopies tended to be longer than those in the well-exposed canopies, while their secondary shoots had a lower mass and shorter length. This is in accordance Hunter & Visser (1990a) who found a non-significant decrease of the primary shoot length as a result of defoliation. This apparent decrease may facilitate the diversion of photosynthetates to other parts of the vine.

Canopy management did not affect the primary shoot growth of the underdeveloped shoots, probably because they were too short to be topped, whereas defoliation on these shoots would also have been restricted. A non-significant increase in the number of lateral shoots tended to occur on underdeveloped shoots in the well-exposed canopies, which was in agreement with Hunter (2000). It seemed that exposure to sunlight stimulated the development of lateral shoots, even without primary shoots being topped. Laterals of underdeveloped shoots in the shaded canopies tended to have a higher average length, which could be ascribed to the stimulating effect of shading on shoot growth (Keller & Hrazdina, 1996) or a reduction as a result of photomorphogenesis. As the mass of these secondary shoots did not differ between the canopy treatments, the well-exposed canopies induced thicker secondary shoots with probably a higher translocatory potential.

The increase in the mass of normally developed primary shoots after véraison could probably be ascribed to shoot maturation and reserve accumulation. As the mass of the underdeveloped primary shoots did not increase to the same extent, it seems evident that the above-mentioned processes did not occur to the same degree. The decrease in primary shoot mass between four and five weeks after véraison is possibly due to the translocation of water from the shoots to other parts of the vine, such as the clusters. The normal seasonal development of the underdeveloped shoots seemed to be delayed, which explains the higher moisture percentage found in these shoots five weeks after véraison (data not shown).

The balance between vegetative and reproductive growth in underdeveloped shoots was obviously disrupted, resulting in a delay in the ripening (starch accumulation and lignification) of vegetative tissue. The strength of reproductive

sink tissue was most probably increased on these shoots as compared to normally developed shoots. This would, however, seriously affect growth and production of the whole vine in the following season, particularly if these shoots were to be used as spurs.

Although the exact position of the secondary shoots on the primary shoots was not noted, it could be assumed that in the case of the underdeveloped (thus untopped) shoots, the majority of the secondary shoots developed in the basal part of the canopy and in the cluster region. This assumption is based on the average length of the shoots (±50 cm) and the statement of Carbonneau *et al.* (1997) that "the first basal third of the foliage...corresponds to the zone of frequent occurrence of laterals;...". Therefore secondary shoots of underdeveloped shoots may contribute to the development of a denser and more shaded cluster region.

With normally developed shoots, the topping treatment probably stimulated the formation of secondary shoots in the apical part of the primary shoot due to the removal of apical dominance caused by the inhibitory effect of growth regulators such as auxin (Hunter, 2000). Secondary shoots were therefore most probably positioned over the whole length of the primary shoot, which was regarded as important for the optimal efficiency of the canopy and contribution to the clusters (Hunter, 2000).

Lignification and starch content

After a massive growth rate of primary shoots during late spring (Coombe, 1992), the vegetative growth rate of shoots decrease during the summer, with internode elongation ceasing progressively from the basal to the apical part of the shoot. Ideally, according to Archer (1988), shoot growth should stop at véraison in a balanced vineyard.

After elongation, shoot maturation (formation of periderm) and reserve accumulation commenced, with a sharp increase towards the post-harvest stage (Hunter *et al.*, 1995a). This is in accordance with Phenological Stage No.41 of Eichhorn & Lorenz, 1977, according to Coombe (1992). They regarded wood maturation as complete after harvest. Thus, lignification and reserve accumulation occur at the same time as grape ripening, which should result in competition between the vegetative and reproductive organs of the vine.

Maturation of the normally developed shoots was far more advanced at véraison than underdeveloped shoots. Maturation of the latter also did not occur at the same rate than that of the normal shoots during grape ripening. Therefore it may be assumed that a stronger competition occurred in underdeveloped shoots between shoot and grape ripening and that both processes were probably negatively affected. In order to maintain longevity, grape ripening should occur without any detrimental effect on growth and development in other parts of the vine (Hunter & Archer, 2001b), such as shoot maturation and reserve accumulation.

Because of leaf age differences, the import:export ratio in the canopies of field grown vines continuously change during the growth season (Hunter *et al.*, 1994), meaning that, depending on the time during the growth season, different leaves are sources and different organs sinks. The different leaf age groups therefore play a major role in the continuous changing of the import:export kinetics in the canopy as the growth season progresses (Hunter & Le Roux, 1997).

In basal leaves, CO_2 assimilation increased until the berries reached pea size, whereafter it declined to low rates during the ripening and post-harvest periods (Hunter *et al.*, 1994). This was probably due to the ageing effect, as Kriedemann (1977) noted a reduction in both the photosynthetic efficiency and capacity of older leaves. The photosynthetic rate of the apical leaves was higher than that of the basal leaves after véraison, increasing slightly at ripeness and decreasing after harvest (Hunter *et al.*, 1994).

According to Koblet (1977), the most basal leaves on a shoot export most of their carbohydrates basipetally throughout the growth season. After véraison, as berry ripening proceeded, it was found that the predominant movement of photosynthetates from apical leaves was to the berries (Koblet, 1977), while assimilates for growth and development of the clusters at ripeness were mainly obtained from leaves in the cluster region (Hunter & Visser, 1988a).

After cessation of vegetative growth, both supply and demand for photosynthetates decreased (Hunter & Visser, 1990a), which explains the very slow rate of assimilate translocation noted by De la Harpe (1983) and Hunter *et al.* (1995a) at ripeness. According to De la Harpe (1983) not even the storage organs, such as the trunk, cordon arms and roots, constituted very strong sinks. The persisting CO_2 assimilation by basal leaves during ripening (Hunter *et al.*,

1994) sustained carbohydrate supply while the demand decreased. This led to an increase in the supply:demand ratio in the vine (Hunter *et al.*, 1995a). The assumption may thus be made that because the sink demand decreases, sucrose accumulates in the basal parts of the shoot where it is then metabolised to starch and stored. This partly explains the higher starch content of the basal part of the shoot compared to the rest of the shoot.

It should also be taken into account that the leaves from the middle, and in particular, the apical parts of the shoots are still actively transporting sucrose to the ripening clusters five weeks after véraison, which further explains why less assimilate is available for reserve accumulation in those parts of the shoot. In the case of normally developed shoots, the assimilate supply from the leaves was probably enough to adequately ripen the clusters and accumulate starch simultaneously, which could be the reason for the more uniform starch content found in these shoots. On the other hand, the supply of the leaves of the underdeveloped shoots was probably not enough to satisfy the demand of the ripening clusters as well as the shoots.

Although the basal starch concentration of the underdeveloped shoots was significantly higher than that of the normally developed shoots, the total starch content should also be taken into account (Fig. 7). Normally developed shoots have significantly more total starch reserves in the basal parts than underdeveloped shoots, while exposure of the canopy ostensibly led to higher total starch content for the former shoots. This is mainly due to the higher dry shoot mass in the case of the normally developed shoots as well as the shoots from the well-exposed canopies (data not shown). These stored reserves in the basal part of the shoot play an important role in growth and development of vegetative as well as reproductive tissue in the following season (Hunter *et al.*, 1995a), particularly when a spur pruning system is used.

Primary leaf development and growth

No difference in the number of primary leaves per shoot for the different shoot types was found, except for the normally developed shoots in the shaded canopies that had more leaves per shoot, albeit not significantly. The longer shoot lengths found in the shaded canopies most probably contributed to this phenomenon. It was further found that the primary leaves of the normally developed shoots in the shaded canopies comprised a larger percentage of the total leaf area per shoot than in the exposed canopies, due to the higher number

of leaves per shoot as well as the larger mean primary leaf area. This is in accordance with Keller & Hrazdina (1996) who found that low light intensity stimulated individual leaf area expansion.

Primary leaves from underdeveloped shoots in shaded canopies also seemed to have a larger mean area than those in the exposed canopies. The result being a non-significant larger contribution of the primary leaves to the total leaf area per underdeveloped shoot in the shaded canopies (as there was no significant difference in the number of primary leaves per shoot between the canopy treatments).

Although the normally and underdeveloped shoots had similar numbers of primary leaves per shoot, the primary leaves of the normal shoots comprised a much larger percentage of the total leaf area per shoot. This was explained by the much larger primary leaves found on the normally developed shoots.

Secondary leaf development and growth

The higher number of secondary leaves on the normally developed shoots compared to the underdeveloped shoots was expected, as they had significantly more and longer secondary shoots. The longer secondary shoots could also be the reason for the difference between the canopy treatments in the case of the normally developed shoots.

The larger mean secondary leaf area of the normally developed shoots in the shaded canopies supports the statement of Keller & Hrazdina (1996) that low light intensities stimulate individual leaf expansion. On the contrary, secondary leaves of the underdeveloped shoots in the well-exposed canopies tended to be somewhat larger, which could possibly be explained by the better development of the secondary shoots under those conditions. It was, however, not statistically significant and did not make any difference in the composition of the total leaf area per underdeveloped shoot.

According to Poni & Giachino (2000) the assimilation rate of the secondary leaves increased with the lateral shoot size and decreased the more primary leaves were retained with trimming. If their findings were to be true in this case as well, it could be expected that the secondary leaves on the normally developed shoots from the vines with exposed canopies will have the highest assimilation rates of all the shoot-canopy treatment combinations and will

therefore make a large contribution to the total photosynthetic activity of the shoot.

Hunter (2000) stated that the activity of secondary leaves in the canopy makes an important contribution in the attainment of maximum yield and grape quality. Not only the leaf area as such, but also the composition, should be taken into account as it plays a critical role in the efficiency of the canopy and the nourishing of the clusters. Therefore, the normally developed shoots could have a greater potential for producing a higher yield with better quality than the underdeveloped shoots, as they have a more desirable leaf area composition in addition to the larger total leaf area per shoot.

Leaf area:leaf mass ratio

It was found that leaves from the well-exposed canopies were thicker than those from the shaded canopies, while the normally developed shoots also had a higher leaf area:mass ratio than the underdeveloped shoots. Higher levels of PPFD were measured in the well-exposed than in the shaded canopies (Fig. 13). Basal leaves of normally developed shoots were also more exposed to sunlight than those of underdeveloped shoots. According to Marini & Marini (1983), a strong correlation existed between the specific leaf mass and the PPFD in the canopy, while Keller & Hrazdina (1996) found stimulated individual leaf area expansion under low light intensities. This would explain why thicker leaves were found in canopies and on shoots that were better exposed to sunlight.

According to Marini & Marini (1983), Crookston *et al.* (1975) noted a reduced differentiation of palisade and mesophyll cells in shade-grown leaves, which could have been partly responsible for the reduced net photosynthesis found. It could therefore be expected that the difference in the leaf area:mass ratio between the shoot types and the canopy treatments will have an important effect on the physiological activity of the individual shoots as well as the efficiency of the respective canopies.

6. CONCLUSIONS

Compared to the underdeveloped shoots, the normally developed shoots were longer and thicker with more and longer secondary shoots distributed over the whole length of the shoot. The latter was found to be important for the optimal

efficiency of the canopy. Within canopy treatments, normally developed shoots from the shaded canopies were longer and thinner that in the exposed canopies. More and longer secondary shoots developed on the normal shoots in the more exposed canopies. Secondary shoots on the shoots that were underdeveloped also seemed to be thicker in the exposed canopies. The thicker shoots can be a possible indication of a higher physiological potential, within limits.

Periderm development (lignification of the shoot) in normal shoots occurred earlier in the season and maturation of the shoots was thus not in such strong competition with grape ripening than it seemed to be in the case of underdeveloped shoots. Higher levels of starch formation and accumulation occurred in the normally developed shoots, while reserves were also more evenly distributed over the whole length of the shoot. The total starch content of the shoots from the well-exposed canopies was also higher on a per shoot basis, which may have a significant effect on the initial growth of the following season. The leaves of the normally developed shoots were better able to supply assimilates to both the shoots and grapes for their ripening, especially in the well-exposed canopies. In order to maintain longevity of the vine (and also the functionality of individual spurs) grape ripening should occur without any detrimental effect on other processes in the vine, such as reserve accumulation. This did not happen in the case of the underdeveloped shoots, as reserve accumulation seemed to be impaired by grape ripening processes.

Significant larger primary leaves were found on normally developed shoots compared to underdeveloped shoots, although no difference in the number of leaves per shoot was found. Secondary leaves on the normally developed shoots were found to be more numerous and larger than on the underdeveloped shoots, while more secondary leaves were found on normal shoots from the exposed compared to the shaded canopies. Primary as well as secondary leaves were found to be larger in the shaded compared to the well-exposed canopies, whereas the leaf area:mass ratio were lower in the exposed canopies.

The primary and secondary leaves of the normally developed shoots made an almost equal contribution to the total leaf area per shoot, whereas the primary leaves of the underdeveloped shoots made a noticeably higher contribution. Therefore, the normally developed shoots may have a greater potential for producing a higher yield of better quality than the underdeveloped shoots, without impairing the longevity of the spur.

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CHAPTER 4

RESEARCH RESULTS

THE EFFECT OF SHOOT HETEROGENEITY ON PHYSIOLOGICAL PARAMETERS OF SHIRAZ/RICHTER 99 GRAPEVINES

1. ABSTRACT

In this study the physiology of normally and underdeveloped shoots was compared in an attempt to quantify the effect of shoot heterogeneity in a Shiraz/Richter 99 vineyard. The field trial was performed in the Stellenbosch area, Western Cape, South Africa. Comparisons based on certain physiological parameters were made between normally and underdeveloped shoots from shaded and well-exposed canopies. In the first five weeks after véraison, photosynthesis, transpiration, stomatal conductivity and water use efficiency (WUE) decreased as berry ripening progressed, while the internal CO_2 levels in the leaves increased. The improving effect on physiological activity induced by exposed canopies became apparent from the third week after véraison. Canopy management practices clearly improved the functionality of the leaves. Up to the third week after véraison, it seemed as if the total effective leaf area per shoot rather than the physiological functionality per unit leaf area should be considered the more important, since differences in physiological activity between leaves from normally and underdeveloped shoots only became apparent in the third week after véraison. From the third week after véraison, the larger effective leaf area per shoot as well as the higher physiological activity per unit leaf area led to the assumption that higher levels of photosynthetates are produced in leaves from normally developed shoots that from underdeveloped shoots. No positive correlation between the photosynthetic activity and the chlorophyll concentration of the leaves was found five weeks after véraison. Equal amounts of chlorophyll.cm^{-2} and a non-significant difference in the assimilation number were calculated for the leaves from normally and underdeveloped shoots with no significant differences between the shaded and well-exposed canopies. It is therefore rather the effective area per leaf or per shoot than the chlorophyll concentration or activity that is responsible for any differences in the photosynthetic productivity of the leaves from normally and underdeveloped shoots in the shaded or well-exposed canopies. The size and quality of the yield from normally developed shoots is thus expected to be higher than that from the underdeveloped shoots.

2. INTRODUCTION

In order to meet the requirements of the national and international markets, it is essential that yields must be maximised without impairing the quality of the yield or the longevity of the vine.

According to Carbonneau (1995) the yield, berry maturation and wine quality are dependent on the canopy structure. The leaf area (LA):trellis surface area (SA) ratio correlated very well with must and wine analysis and sensory scores (Smart, 1982), as well as with the canopy microclimate (Smart *et al.*, 1985). The latter was defined as the signal for the physiological functioning of the canopy and was found to be dependent on the amount and spatial distribution of the leaf surface (Archer & Strauss, 1989a). According to Carbonneau *et al.* (1997) the exposed leaf area that was able to reach the photosynthetic potential, and thus ensured a largely positive carbon balance for the plant beyond its own carbon requirement, was a good estimation of the physiological potential of the canopy. This statement could possibly be adjusted so that the leaf area on a shoot that is able to reach its photosynthetic potential is a good estimation of the physiological potential of that specific shoot.

It is well known that the quality of a cluster is directly proportional to the physiological quality of its shoot (Archer, 2001). Individual leaves should thus be maximally exposed so that photosynthetic conditions can be optimal for each leaf (Hunter *et al.*, 1991). Although genetic factors set an upper limit to photosynthetic capacity, observed instantaneous rates of photosynthesis are more commonly dictated by environmental conditions such as water supply, light, temperature, CO_2, and O_2 as well as internal control mechanisms that affect overall demand for photosynthetates and partitioning of assimilates within the vine (Huglin, 1972, according to Kriedemann, 1977).

In the photosynthetic reaction water is biochemically combined with CO_2 during the production of carbohydrates. This water represents less than one percent of the total water absorbed by the roots – the remaining percentage is lost during the process of transpiration (Kriedemann, 1977). Leaves thus need to assimilate atmospheric CO_2 while minimising evaporation loss. Stomata fulfil this regulatory function by opening in response to light exposure or CO_2 depletion within the leaf and closing under low light intensities and when the evaporative demand

exceeds the water supply. The decrease in stomatal aperture reduces the uptake of CO_2 with the resultant decrease in photosynthesis (Smart, 1974).

The efficiency of the leaves was dependent on the amount and intensity of sunlight interception (Hunter, 1991). The more the leaves were exposed to PPFD, the higher the rate of photosynthesis, up to a certain point (Archer, 1988). Optimal photosynthesis occurred at 704-1100 $\mu E.m^{-2}.s^{-1}$ (Champagnol, 1984). At too high light intensities, the stomata closed with a resultant decline in photosynthesis. On the other hand, as shading increased, the photosynthetic rate per unit area decreased (dense canopies, due to excessive vegetative growth, led to sub-optimal canopy microclimates that proved to be detrimental to the photosynthetic rate of the whole canopy) (Hunter & Visser, 1988; Hunter *et al.*, 1991).

There exists a linear relationship between radiation and temperature (Smart, 1987). It was found that radiation (be it intensity or duration) increased the temperature of the exposed leaves, which led to an increase in photosynthetic activity. The optimum temperature for photosynthesis is generally regarded as 25°C (Kriedemann, 1977; Alleweldt *et al.* 1982), while under field conditions variation in temperature between 16°C and 29°C did not affect the rate of photosynthesis (Archer, 1981). According to Kriedemann (1977) vine leaves suffer more from desiccation than from high temperature as such. As long as the leaf is hydrated, it can withstand temperatures up to 48°C. Temperatures higher than the optimum affect enzyme activity negatively (Hunter, 1991). Excessive temperatures cause instability of enzymes and tissue desiccation (Kriedemann, 1977).

In higher plants, the light absorbing pigments embedded in specialised internal membranes (called the thylakoid system) consist largely of two kinds of chlorophylls of which the content of chlorophyll *a* is usually two to three times that of chlorophyll *b*. According to Hunter (2001, and references therein), light promotes some reactions during chlorophyll synthesis, such as the production of delta-amino levulinic acid (ALA), the precursor of protochlorophyllide a and chlorophyll *a*, and the conversion of protochlorophyllide *a* to chlorophyll *a*. The conversion of chlorophyll *a* to chlorophyll *b* occurs in either light or darkness.

Although the synthesis of chlorophyll is light depended, higher chlorophyll concentrations were found for interior leaves than peripheral, sun-exposed peach

leaves (Kappel & Flore, 1983; Marini & Marini, 1983). Hunter & Visser (1989) found higher chlorophyll concentrations for the interior, recently matured basal leaves at the early developmental stages, while maximum chlorophyll *a* and *b* concentrations were reached later during the growth season as the leaves were progressively situated towards the periphery of the canopy and more to the apical part of the shoot. They ascribed the variation in chlorophyll concentration of the different leaves during the growth season to the differences in leaf age.

During the course of this study, the possible effect of leaf age on the chlorophyll content of the leaves were minimised, since all the primary leaves on a shoot were analysed together to determine the chlorophyll concentration. Thus, mainly the effects of the degree of canopy exposure and shoot development were determined.

According to Hunter & Visser (1989) no consistent relationship existed between chlorophyll concentration and photosynthetic activity of exterior leaves. A better relationship was, however, found between the chlorophyll concentration and the photosynthetic activity of mature, interior canopy leaves that were exposed to lower light conditions. They further stated that factors such as the source:sink relationship, feedback inhibition of photosynthesis by end products and internal resistance to CO_2 transfer within the leaf were probably more regulatory to photosynthetic activity than chlorophyll concentration and light intensity.

The total leaf area in relation to crop load is a factor that may affect the photosynthetic rate of individual leaves (Petrie *et al.*, 2000). Source limitation of photosynthesis occurred when the capacity of the assimilate supplying reactions was inadequate for the demand of the sink tissues (Iacono *et al.*, 1995). In the grapevine this usually happens in the case of a high reproductive to vegetative growth ratio (Bravdo & Naor, 1995) when assimilate production of the leaf area is insufficient to meet the demand from the clusters. Sink limitation of photosynthesis, on the other hand, occurred when the rate at which assimilates were utilised and/or stored was less than that at which it was produced and supplied to the sink tissues (Baysdorfer & Bassham, 1985, according to Iacono *et al.*, 1995). This can be called under-cropping in the grapevine where there is a high vegetative to reproductive growth ratio (Bravdo & Naor, 1995). The result being an accumulation of photosynthetic end products in the leaves and an increase in the internal CO_2 concentration with a decrease in the photosynthetic activity.

In this study, physiological parameters were determined in an attempt to quantify differences that may exist in the functioning of normally and underdeveloped shoots under well-exposed and shaded conditions.

3. MATERIALS AND METHODS

Experimental vineyard

A seven year old *Vitis vinifera* L. cv. Shiraz, clone SH1A, grafted onto Richter 99 (*Vitis Berlandieri* x *Vitis rupestris*), clone RY2A, vineyard was used for this study. The vineyard is situated at the experimental farm of the Agricultural Research Council (ARC) Infruitec-Nietvoorbij near Stellenbosch in the Western Cape (Mediterranean climate). The vines are spaced 2.75 m × 1.5 m on a Glenrosa soil with a western aspect (26° slope) and trained onto a 7-wire lengthened Perold trellising system with movable canopy wires (VSP). Rows were orientated in a North-South direction.

Micro sprinkler irrigation was applied at pea size berry and at véraison. Pest and disease control was applied during the growth season according to the standard program of the ARC.

Experiment design

The experiment was laid out as a completely randomised 2×3×2 factorial design. The three factors were: degree of canopy exposure (well-exposed and shaded canopies); ripening stages (two weeks, three weeks and five weeks after véraison); and level of shoot development (normally and underdeveloped shoots). There were three replications for each of the 12 treatment combinations.

Shaded canopies were only shoot positioned and topped, whereas additional suckering and leaf thinning were applied in order to create well-exposed canopies. Selection of underdeveloped shoots was based on length and comparative lack of lignification at véraison.

Measurements

Photosynthesis and transpiration measurements: [Also described in Hunter & Visser (1988)]. Rate of photosynthesis (mg $CO_2.dm^{-2}.h^{-1}$), stomatal resistance ($s.cm^{-1}$), rate of transpiration ($\mu g\ H_2O.cm^{-2}.s^{-1}$), photosynthetic photon flux density

($W.m^{-2}$), percentage relative humidity, internal CO_2 (μbar) and leaf temperature (°C) were measured in the vineyard with an ADC portable photosynthesis meter (The Analytical Development Co., England). The apparatus consists of an infrared CO_2 analyser, a data logger, a Parkinson broad leaf chamber and air supply unit. The volume of the chamber is 16 cm^3 and the area 6.25 cm^2. The length of the air supply tube is 4 m. Radiation was measured using a quantum sensor with filters providing response from 400 nm to 700 nm. The maximum vapour pressure (E_{max}) was taken as two, while the airflow rate through the open system was adjusted to 300 $cm^3.min^{-1}$. Measurements were taken at 10:00 on the day scheduled (31 January, 8 February and 21 February 2002). Three replications were used. Sun leaves in the basal (first three leaves above the bunches) position on the shoot were measured in all the cases whereafter the measurements obtained were converted to molar units per square metre per second, i.e. rate of photosynthesis ($\mu mol.m^{-2}.s^{-1}$), stomatal conductance ($mmol.m^{-2}.s^{-1}$), rate of transpiration ($mmol.m^{-2}.s^{-1}$), photosynthetic photon flux density ($\mu mol.m^{-2}.s^{-1}$), percentage relative humidity, internal CO_2 (μbar) and leaf temperature (°C).

The water use efficiency ratio (WUE) was calculated by dividing the rate of photosynthesis by the transpiration rate.

Chlorophyll determinations: [Also described in Hunter & Visser (1989)]
A representative leaf sample of 5 g (fresh weight) was cut into pieces of 1 cm^2. The leaf material was added to 100 cm^3 80% aqueous acetone containing 0.1 g $CaCO_3$ and macerated with a Janke & Kunkel Ultra-Turrax T25 macerator at room temperature for 60 seconds at 20 500 rpm. The homogenate was left to settle in the dark at 5°C for 24 h, after which the sediment was completely discoloured. Absorbancies at 645 nm and 663 nm were determined with a LKB Biochrom Utrospec spectrophotometer (II E) using 2 mm quartz cells.

The equations used for the determination of chlorophyll concentration were as follows:

Chlorophyll *a* = $(0.0127A_{663} - 0.00269A_{645}) \times 20\,000 = \mu g.g^{-1}$ fresh mass
Chlorophyll *b* = $(0.0229A_{645} - 0.00468A_{663}) \times 20\,000 = \mu g.g^{-1}$ fresh mass
Total chlorophyll = $(0.0202A_{645} + 0.00802A_{663}) \times 20\,000 = \mu g.g^{-1}$ fresh mass

The determination of the chlorophyll concentration ($\mu g.g^{-1}$) of the fresh leaves was carried out five weeks after véraison in 2002 and 2003. The chlorophyll content per unit leaf area ($\mu g.cm^{-2}$) and assimilation number ($\mu mol\ CO_2.\mu g\ chlorophyll^{-1}.s^{-1}$) was only calculated for 2003, since no leaf mass measurements were carried out in 2002. Leaf areas were measured with a LICOR LI-3100 area meter (Lincoln, Nebraska, USA).

Statistical analyses

Due to the nature of the data, a non-parametric bootstrap analysis was used when it proved to be more practical than factorial ANOVA. The significance of the results was evaluated using 95% confidence intervals. Since there were only three replications per treatment, tendencies, rather than absolute statistical significances, were discussed. During interpretation of the figures, differences were considered significant when no overlapping of the 95% confidence intervals occurred.

4. RESULTS

Photosynthetic parameters (10:00)

Second week after véraison (31/01/2002): No significant difference was found in the level of PPFD received by the basal leaves from normally and underdeveloped shoots (Fig. 1). The degree of canopy exposure did not seem to have a significant effect either (Fig. 2). A larger variation in measurements was found for the underdeveloped shoots compared to the normal shoots (Fig. 3). No difference in the PPFD received by underdeveloped shoots was found between the canopy treatments, while it seemed as if normally developed shoots received higher levels of PPFD in well-exposed compared to shaded canopies (Fig. 3).

No difference was found in the photosynthetic rate of normally and underdeveloped shoots in shaded or well-exposed canopies (Figs. 4 - 6) during this early stage of grape ripening.

The internal CO_2 levels of the leaves from normal and underdeveloped shoots were not statistically different (Fig. 7). No significant difference was found when canopy exposure was considered as the main treatment (Fig. 8). Differences were measured between the shoots in the exposed canopies, while no difference between the shoot types in the shaded canopies was found (Fig. 9). However,

lower average values seemed to be evident in the exposed compared to the shaded canopies.

Stomatal conductivity did not differ between normal and underdeveloped shoots (Fig. 10), although the measurements from underdeveloped shoots showed a higher variability (Figs. 10 & 12). The degree of canopy exposure did not seem to affect the stomatal conductance to a large extent (Fig. 11), except for the underdeveloped shoots where the values seemed to be higher in the shaded than exposed canopies (although not statistically significant) (Fig. 12).

The rate of transpiration showed no differences between normal and underdeveloped shoots (Fig. 13) in shaded or well-exposed canopies (Figs. 14 & 15). Better canopy exposure seemed to reduce the transpiration rate (Fig. 14), but this was mostly due to the reducing effect found for underdeveloped shoots (Fig. 15).

The water use efficiency (WUE) between normally and underdeveloped shoots was similar (Fig. 16). Although not significantly improved, canopy exposure seemed to increase the WUE (Figs. 17 & 18).

Third week after véraison (08/02/2002): The level of PPFD received by the shoots in the respective canopies was significantly less than in the previous week (Figs. 1 & 2). The average PPFD received by the normally developed shoots was higher than that received by the underdeveloped shoots in the shaded and exposed canopies, although the differences were not statistically significant (Fig. 3). Better sunlight penetration, albeit not significant, was induced by the application of the additional canopy management practices (Fig. 2).

The rate of photosynthesis did not seem to decrease from the previous week in the case of the normally developed shoots (Fig. 4). However, the underdeveloped shoots displayed a significant decrease, particularly in the shaded canopies. The leaves from the normally developed shoots photosynthesised at a significantly higher rate than those from the underdeveloped shoots, in the shaded as well as in the exposed canopies (Figs. 4 & 6). Photosynthetic activity of all the shoots seemed to be impaired in the shaded canopies (Fig. 5).

The internal CO_2 levels in the leaves showed an increasing tendency from the previous week (Figs. 7 & 9). Higher internal CO_2 levels were measured in the leaves from the underdeveloped shoots compared to those from the normal shoots in both the shaded and exposed canopies. This difference was found to be more significant in the exposed canopies, while lower internal CO_2 levels in the leaves in the exposed canopies were mostly measured as well (Fig. 9). The increase in CO_2 level in the case of underdeveloped and shaded leaves most probably resulted from a reduction in the functioning of the photosynthetic apparatus under these circumstances, leading to reduced CO_2 consumption.

Similarly to the rate of photosynthesis, the stomatal conductance of the leaves from the normally developed shoots did not change significantly from the previous week, whereas a significant decrease in the case of the underdeveloped shoots was evident (Fig. 10), especially in the shaded canopies (Fig. 12). The leaves from the normal shoots displayed significantly higher stomatal conductance in both the exposed and shaded canopies than those from the underdeveloped shoots (Fig. 12). The measurements were on average a little higher in the exposed canopies than in the shaded canopies (Fig. 11).

Also in the case of transpiration, the rate was stable from the previous week in the normal shoots, while it decreased significantly in the leaves of underdeveloped shoots, especially in the shaded canopies (Figs. 13 & 15). In the exposed canopies in particular, but also in the shaded canopies, significantly higher transpiration rates were measured in the normal shoots compared to the underdeveloped shoots (Fig. 15). Ostensibly higher average rates were measured in the exposed canopies (Fig. 14).

As could be expected from the measured rates of photosynthesis and transpiration, the WUE of the underdeveloped shoots decreased significantly from the previous week (particularly in the shaded canopies), while the ratio remained constant in the case of normally developed shoots (Figs. 16 & 18). The WUE tended to be higher in the exposed compared to the shaded canopies (Fig. 17).

Fifth week after véraison (21/02/2002): Significantly lower levels of PPFD were measured in the basal area of underdeveloped shoots compared to normal shoots, while the PPFD measured on underdeveloped shoots also showed a

much sharper decrease from the previous measurement taken two weeks earlier (Fig. 1). A significantly better sunlight penetration occurred in the exposed compared to shaded canopies when measured for normal shoots compared to underdeveloped shoots (Fig. 3).

The rate of photosynthesis of the leaves on normally and underdeveloped shoots as well as the rates measured in the exposed and shaded canopies were significantly lower than those obtained two weeks earlier (Figs. 4 & 5). In the fifth week after véraison the photosynthetic rate of basal leaves on underdeveloped shoots seemed lower than that of normal shoots in both the shaded and well-exposed canopies, although the difference was not as apparent as two weeks earlier. In the exposed canopies, the normally and underdeveloped shoots displayed significantly higher photosynthetic rates than the shoots in the shaded canopies (Fig. 6).

In correspondence with the rate of photosynthesis, the internal CO_2 levels of the leaves from all the shoots (Fig. 7) in both canopy treatments (Fig. 8) increased from the levels found two weeks earlier. This increase was significant in the shaded canopies, especially regarding the underdeveloped shoots. The internal CO_2 of both the normally and underdeveloped shoots differed significantly between the shaded and exposed canopies in the fifth week after véraison (Fig. 9).

The stomatal conductance of basal leaves on both shoot types decreased from two weeks earlier in the shaded as well as in the exposed canopies. As in the case of photosynthesis, this decrease was significant for the normal shoots in both canopy treatments and for the underdeveloped shoots in the shaded canopies (Fig. 12). Although the stomatal conductance of the leaves on normal shoots compared to that of leaves on underdeveloped shoots (Fig. 10) and for the exposed canopies compared to the shaded canopies (Fig. 11), was higher in the fifth week after véraison, this difference was not regarded as statistically significant.

The transpiration rates measured were higher than would have been expected considering the stomatal conductance (Figs. 13 - 15). Although the rate of transpiration decreased during the two-week period, this was only significant for the normal shoots in the well-exposed canopies. In the fifth week after véraison,

no statistically significant differences were found between the transpiration rates of normally and underdeveloped shoots in shaded or exposed canopies (Fig. 15).

The WUE calculated for both the normally and underdeveloped shoots decreased significantly during two weeks (Fig. 16). No significant difference between the shoots was found in the shaded or exposed canopies in the fifth week after véraison (Fig. 17). This decrease in the WUE was more apparent in the shaded canopies (especially regarding the underdeveloped shoots), while the WUE in the exposed canopies was constantly found to be higher, albeit not statistically significant (Fig. 18).

Over the five-week period after véraison the PPFD and the photosynthetic rate, stomatal conductance, rate of transpiration and the WUE of the leaves decreased, while an increase in the internal CO_2 levels was evident.

Chlorophyll

Chlorophyll a (2002): The chlorophyll *a* concentration of the basal primary leaves of the underdeveloped shoots was significantly higher than that of the primary leaves of the normally developed shoots (Fig. 19a). This also seemed to occur in both shaded and well-exposed canopies (Fig. 20a). In the shaded canopies this difference was significant. Apparently higher chlorophyll *a* concentrations were found in leaves from the shaded compared to the exposed canopies (Fig. 21a).

Chlorophyll b (2002): The chlorophyll *b* concentration in the leaves seemed to show the same tendency than chlorophyll *a*, namely higher concentrations in the shaded canopies and in leaves from underdeveloped shoots. However, none of these differences were found to be statistically significant (Figs. 22a - 24a).

Chlorophyll a:b (2002): No significant difference in the chlorophyll *a:b* ratio between the normally and underdeveloped shoots in either the shaded or well-exposed canopies was found. Although the degree of canopy exposure did not seem to affect this ratio significantly, a more prominent difference between normal and underdeveloped shoots seemed to occur under shaded conditions (Fig. 25a).

Total chlorophyll (2002): As could well be expected from the chlorophyll *a* and *b* data, higher total chlorophyll concentrations were found for the leaves of underdeveloped compared to those of normal shoots in the well-exposed and shaded canopies (Fig. 26a & 27a). In the latter this difference was significant. Apparently higher total chlorophyll concentrations were found in leaves of shaded compared to those of exposed canopies (Fig. 28a).

The above measurements and calculations were repeated in the following year. The difference between the underdeveloped and normally developed shoots were found to be more pronounced, since significantly higher levels of chlorophyll *a*, chlorophyll *b* and total chlorophyll concentrations were obtained in leaves of underdeveloped shoots in both the shaded and well-exposed canopies. In the shaded canopies, significantly higher chlorophyll *a:b* ratios were calculated for normally compared to underdeveloped shoots. The degree of canopy exposure affected the above parameters to a much lesser degree than in 2002 when chlorophyll concentrations seemed to be higher in the shaded canopies (Figs. 19b - 28b).

Chlorophyll.cm^{-2} leaf area (2003): The amount of total chlorophyll.cm^{-2} leaf area was also calculated in 2003 (Fig. 29). No statistically significant differences between the normally and underdeveloped shoots as well as between the shaded and exposed vines could be found, although it seemed as if the average chlorophyll content per unit leaf area tended to be somewhat higher in the exposed compared to the shaded canopies.

Photosynthesis/chlorophyll (μmol.μg^{-1}.s^{-1}) (2003): The rate of photosynthesis per μg chlorophyll showed no significant differences between the normally and underdeveloped shoots, although the average values calculated seemed to be higher in the case of the normal shoots (Fig. 30). The degree of canopy exposure did not seem to affect the normally developed shoots at all, while a non-significant lower average was found for underdeveloped shoots in the exposed canopies.

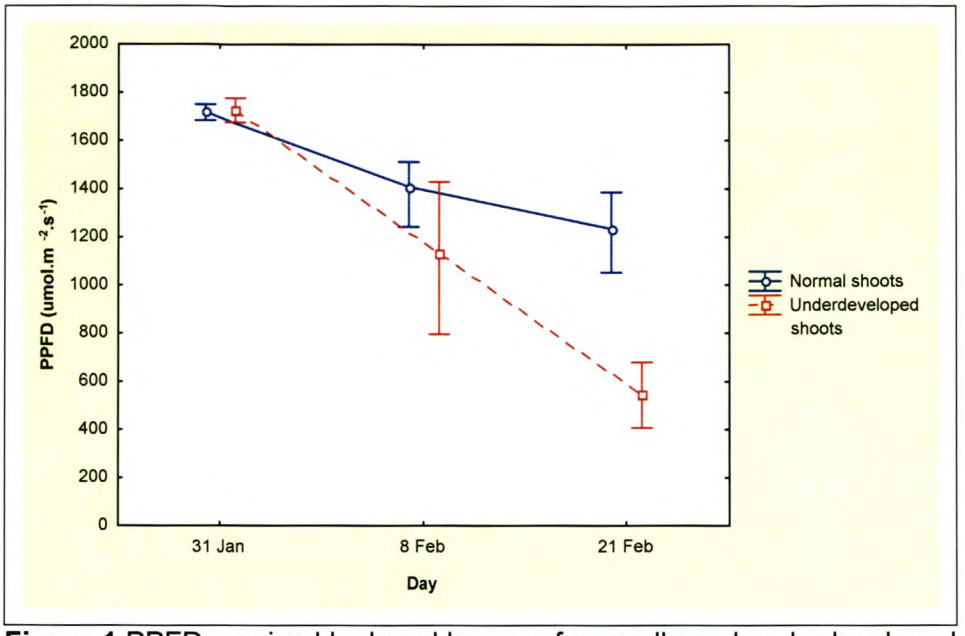

Figure 1 PPFD received by basal leaves of normally and underdeveloped shoots in the second, third and fifth week after véraison. Error bars indicate 95% confidence intervals (bootstrap analysis).

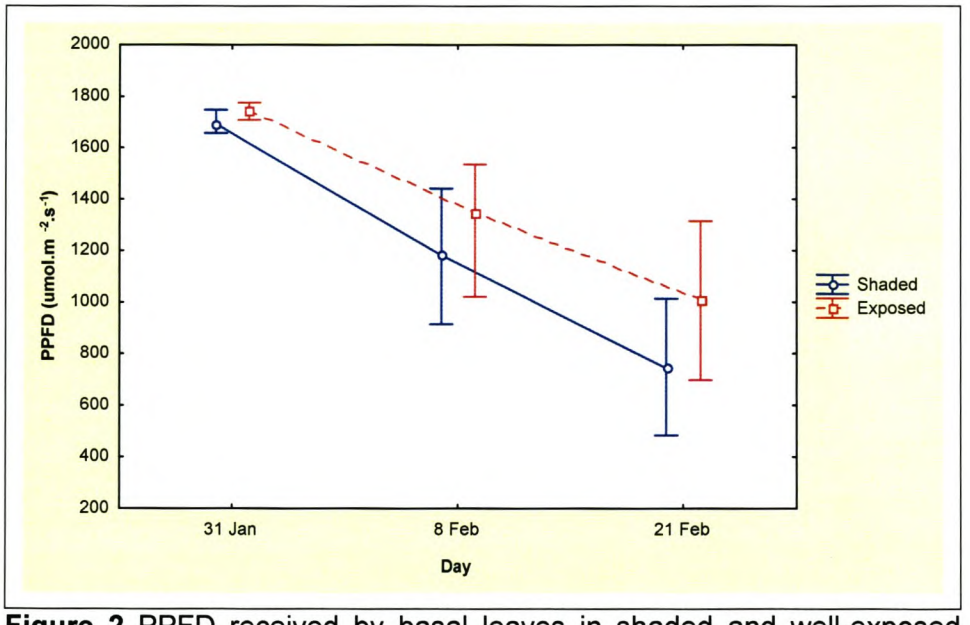

Figure 2 PPFD received by basal leaves in shaded and well-exposed canopies in the second, third and fifth week after véraison. Error bars indicate 95% confidence intervals (bootstrap analysis).

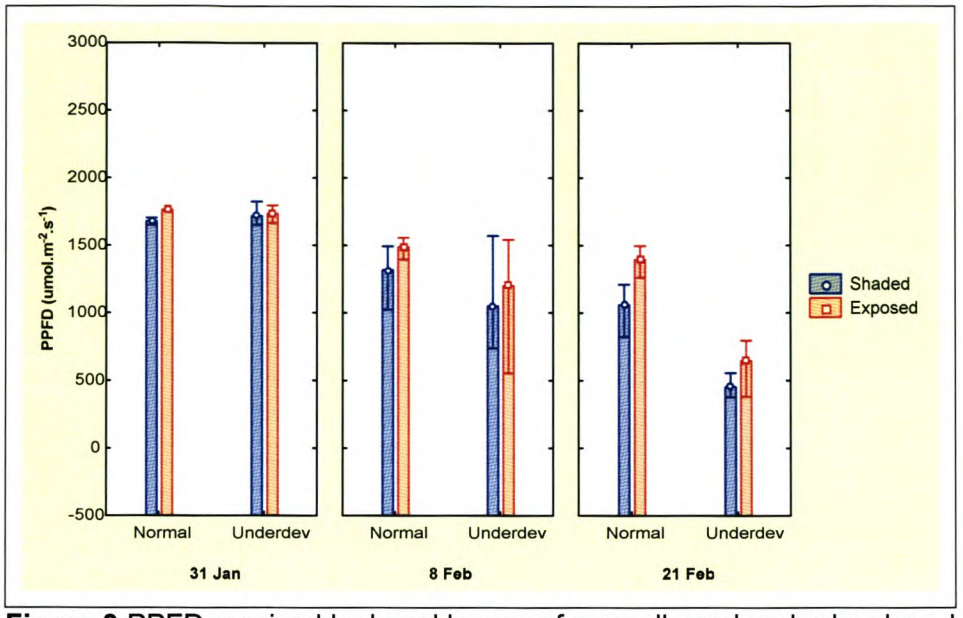

Figure 3 PPFD received by basal leaves of normally and underdeveloped shoots in shaded and well-exposed canopies in the second, third and fifth week after véraison. Error bars indicate 95% confidence intervals (bootstrap analysis).

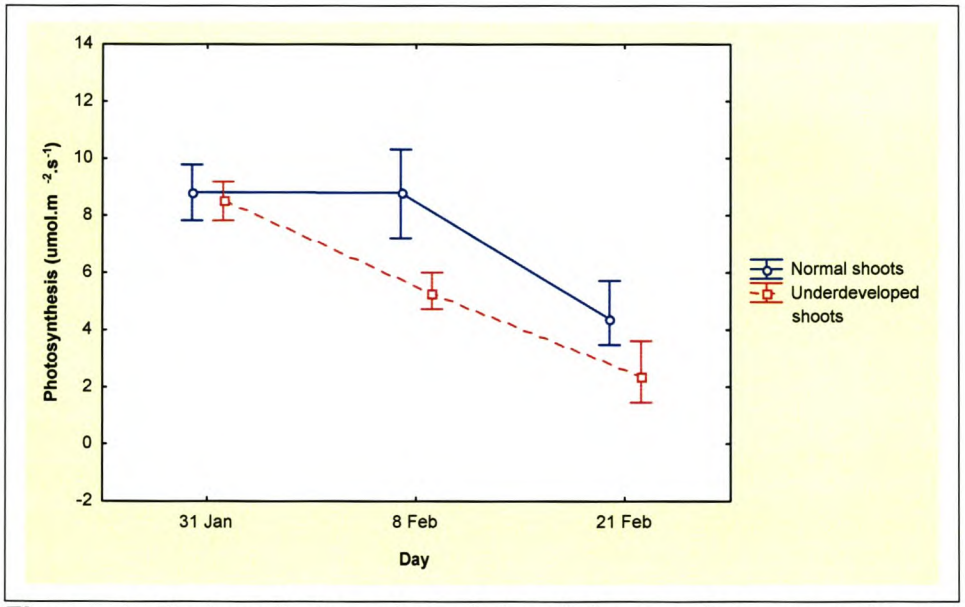

Figure 4 Photosynthetic rates of basal leaves from normally and underdeveloped shoots measured in the second, third and fifth week after véraison. Error bars indicate 95% confidence intervals (bootstrap analysis).

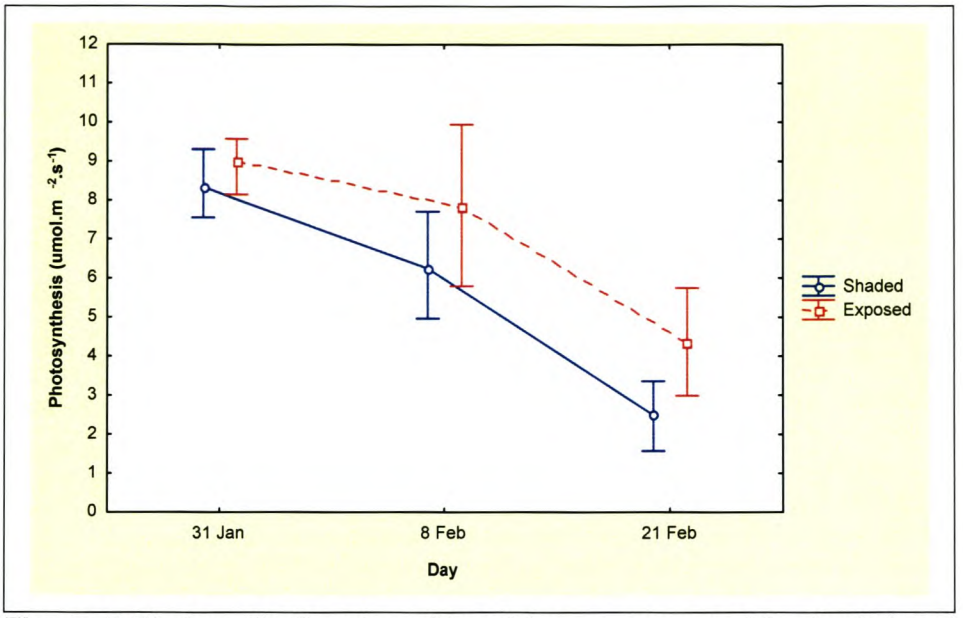

Figure 5 Photosynthetic rates of basal leaves measured in shaded and well-exposed canopies in the second, third and fifth week after véraison. Error bars indicate 95% confidence intervals (bootstrap analysis).

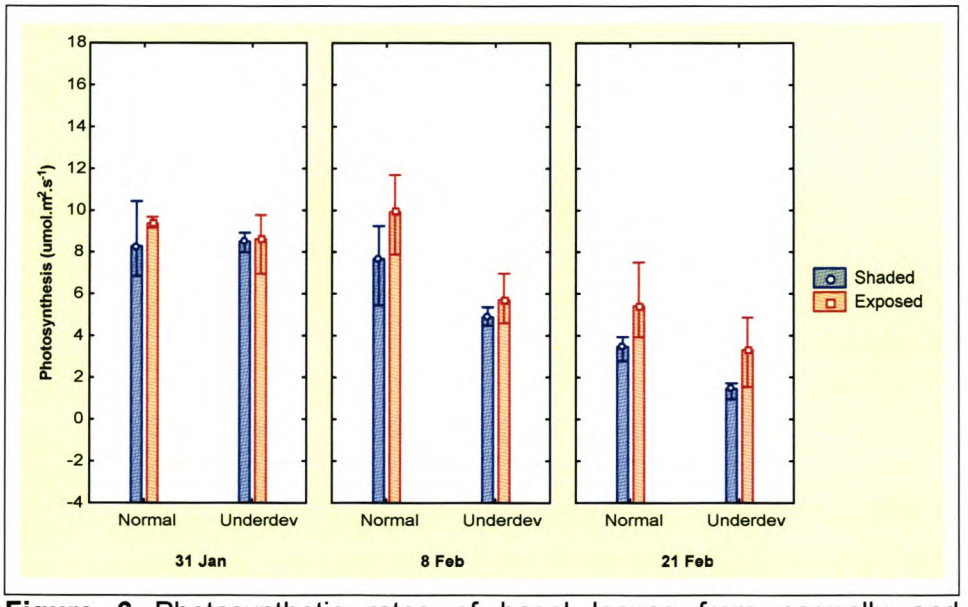

Figure 6 Photosynthetic rates of basal leaves from normally and underdeveloped shoots in shaded and well-exposed canopies measured in the second, third and fifth week after véraison. Error bars indicate 95% confidence intervals (bootstrap analysis).

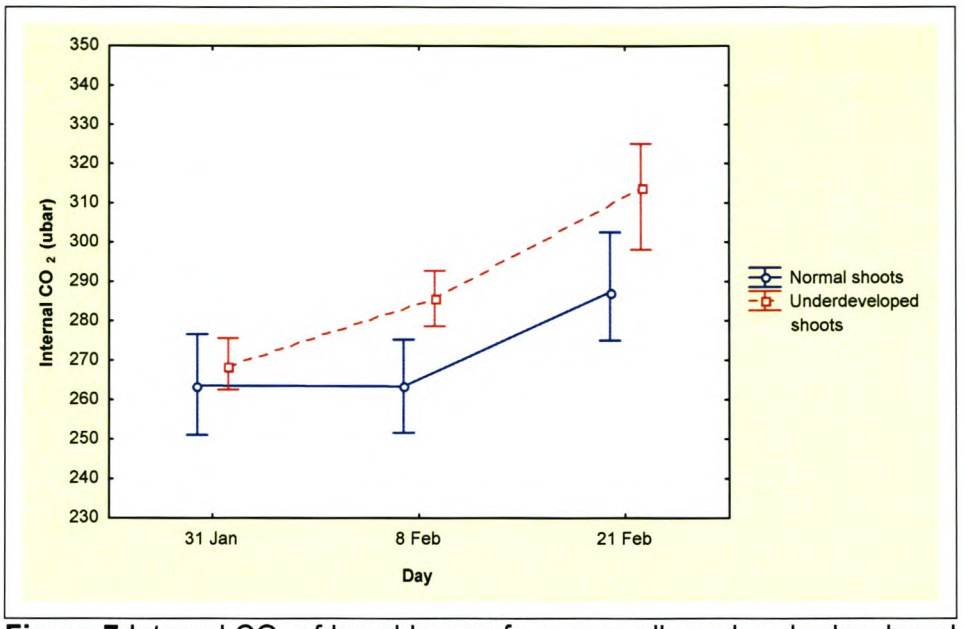

Figure 7 Internal CO_2 of basal leaves from normally and underdeveloped shoots measured in the second, third and fifth week after véraison. Error bars indicate 95% confidence intervals (bootstrap analysis).

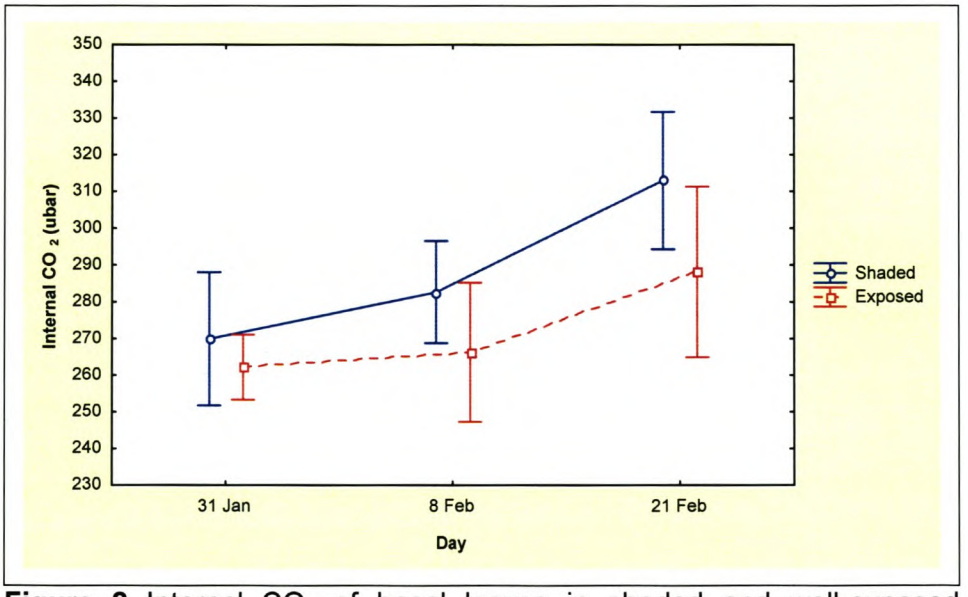

Figure 8 Internal CO_2 of basal leaves in shaded and well-exposed canopies measured in the second, third and fifth week after véraison. Error bars indicate 95% confidence intervals.

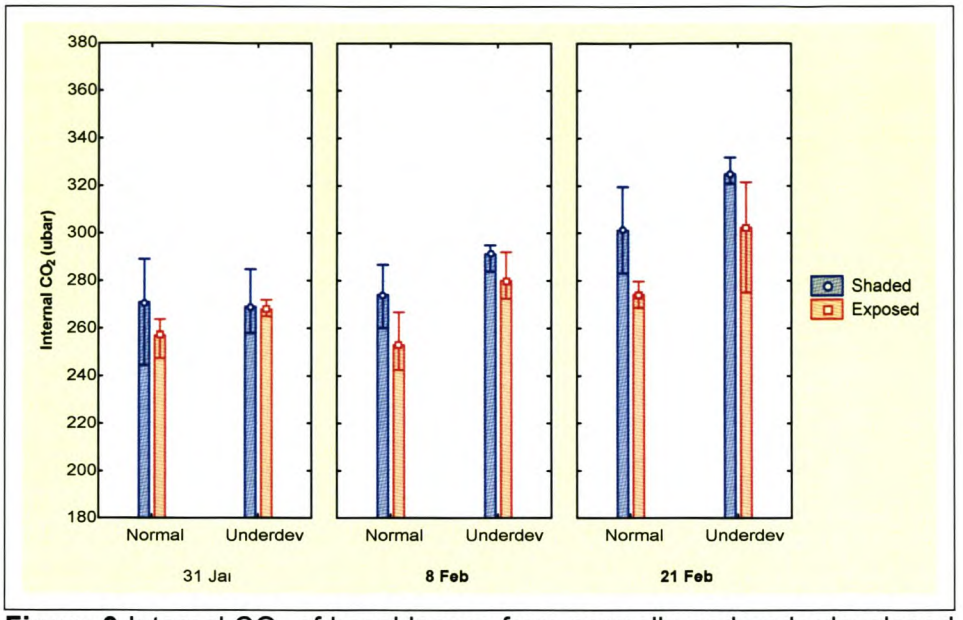

Figure 9 Internal CO_2 of basal leaves from normally and underdeveloped shoots in shaded and well-exposed canopies measured in the second, third and fifth week after véraison. Error bars indicate 95% confidence intervals (bootstrap analysis).

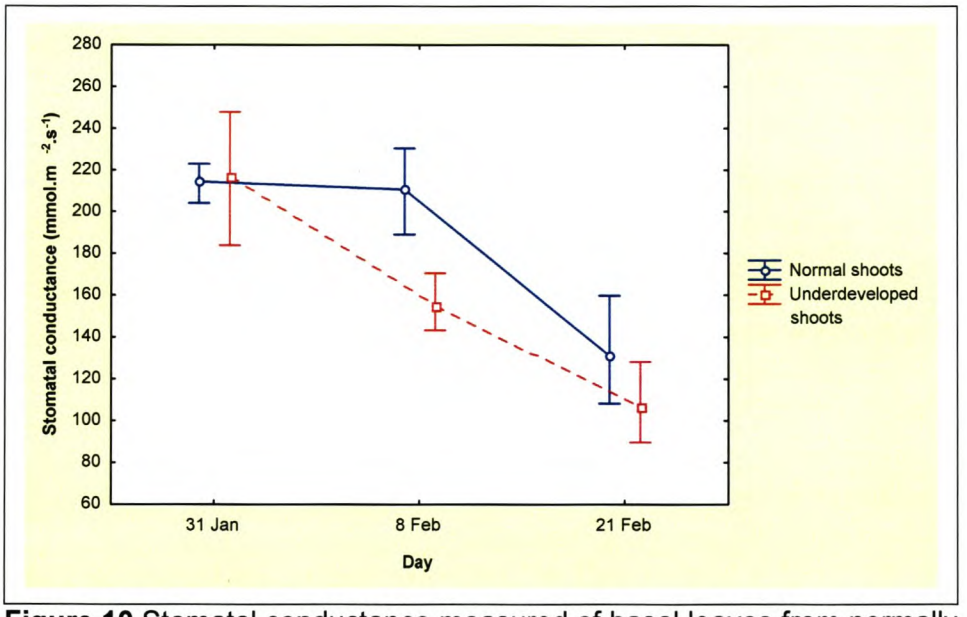

Figure 10 Stomatal conductance measured of basal leaves from normally and underdeveloped shoots in the second, third and fifth week after véraison. Error bars indicate 95% confidence intervals (bootstrap analysis).

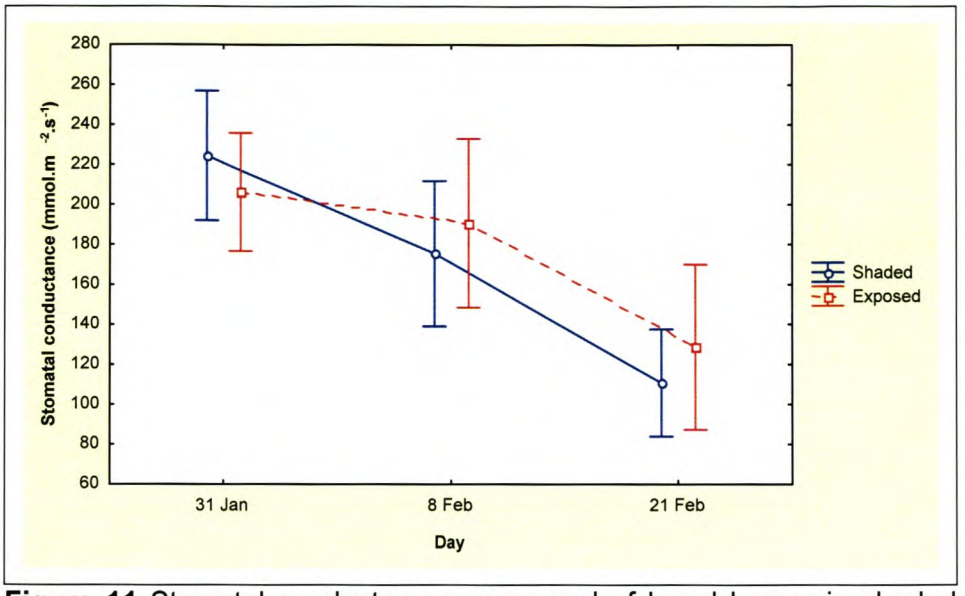

Figure 11 Stomatal conductances measured of basal leaves in shaded and well-exposed canopies in the second, third and fifth week after véraison. Error bars indicate 95% confidence intervals.

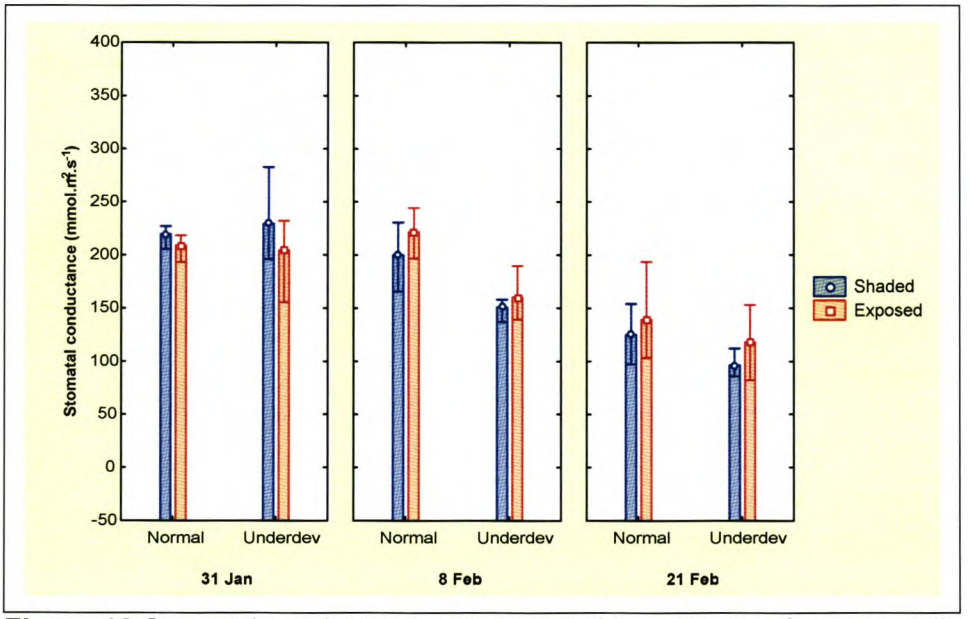

Figure 12 Stomatal conductance measured of basal leaves from normally and underdeveloped shoots in shaded and well-exposed canopies in the second, third and fifth week after véraison. Error bars indicate 95% confidence intervals (bootstrap analysis).

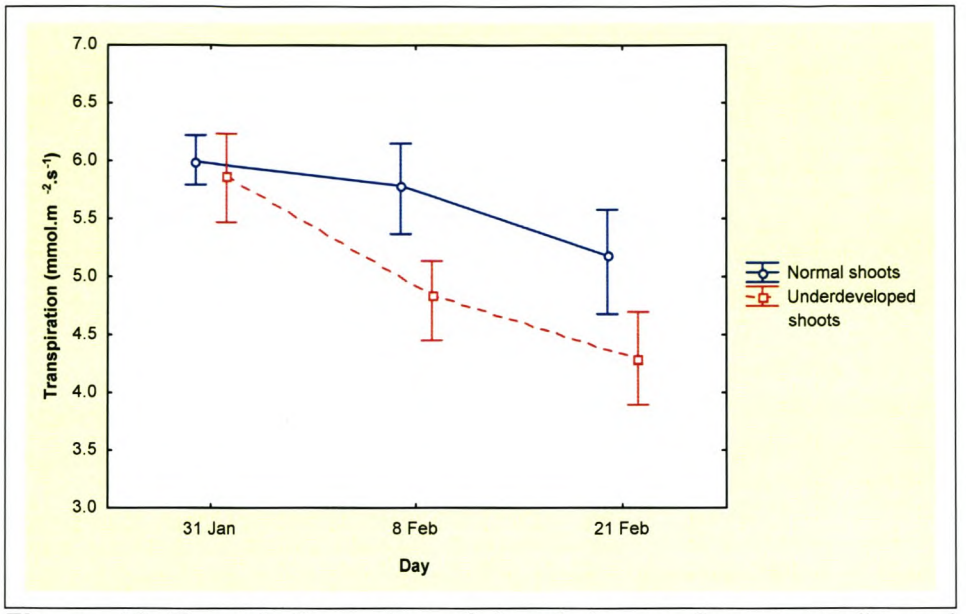

Figure 13 Transpiration rates of basal leaves from normally and underdeveloped shoots in the second, third and fifth week after véraison. Error bars indicate 95% confidence intervals (bootstrap analysis).

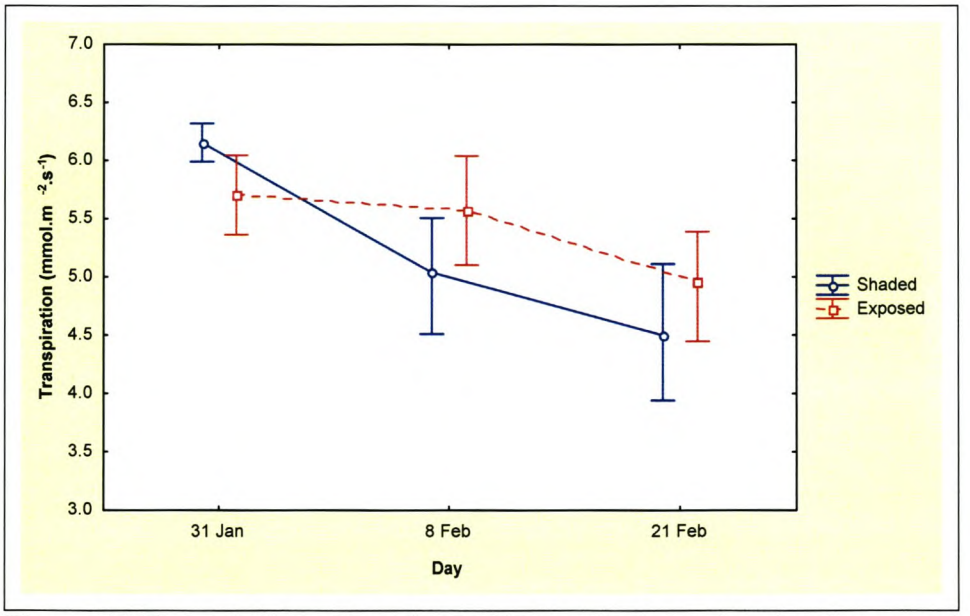

Figure 14 Transpiration rates of basal leaves in shaded and well-exposed canopies in the second, third and fifth week after véraison. Error bars indicate 95% confidence intervals (bootstrap analysis).

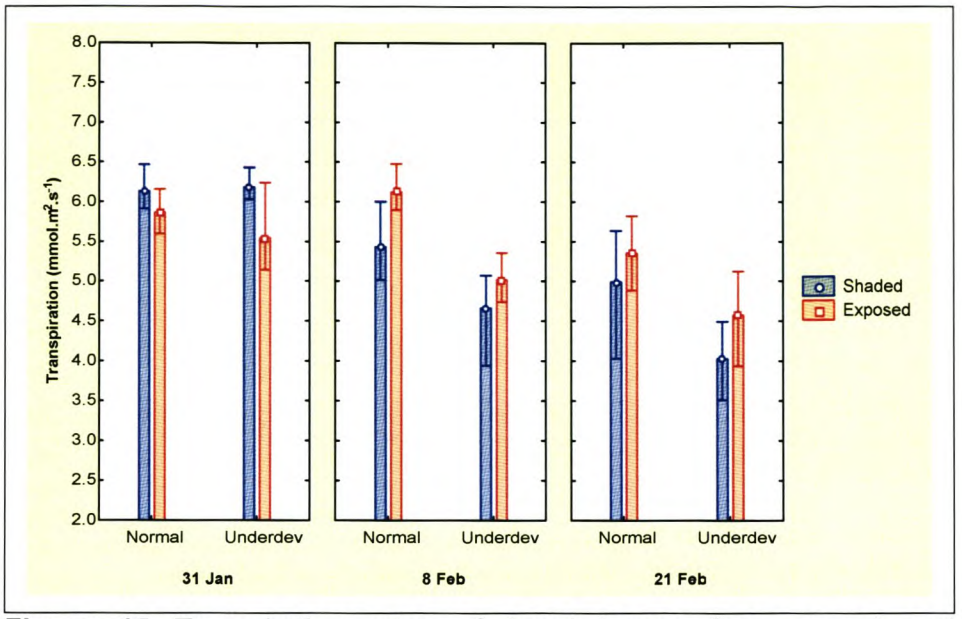

Figure 15 Transpiration rates of basal leaves from normal and underdeveloped shoots in shaded and exposed canopies in the second, third and fifth week after véraison. Error bars indicate 95% confidence intervals (bootstrap analysis).

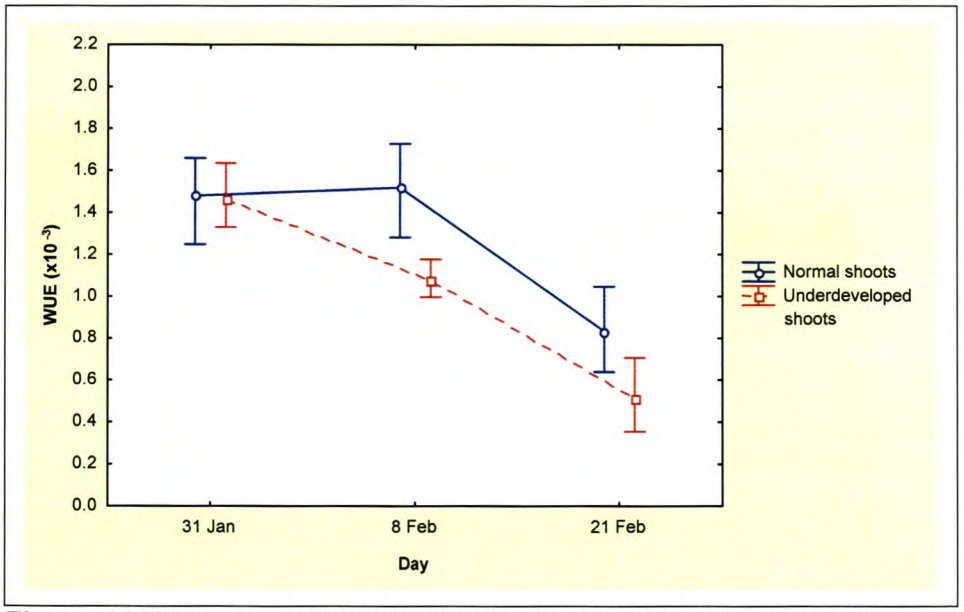

Figure 16 Water use efficiency (WUE) of basal leaves from normally and underdeveloped shoots measured in the second, third and fifth week after véraison. Error bars indicate 95% confidence intervals (bootstrap analysis).

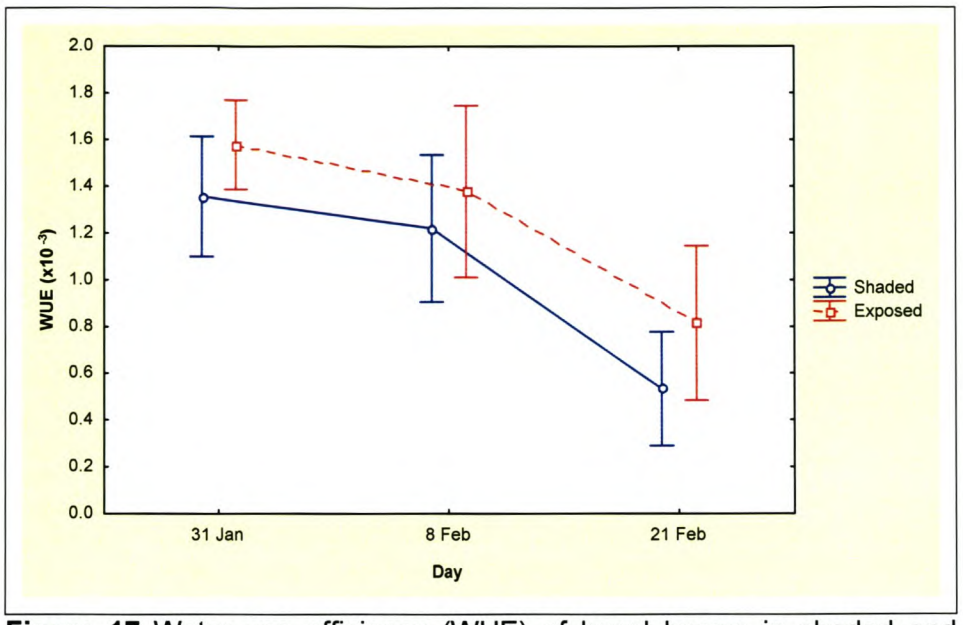

Figure 17 Water use efficiency (WUE) of basal leaves in shaded and well-exposed canopies measured in the second, third and fifth week after véraison. Error bars indicate 95% confidence intervals.

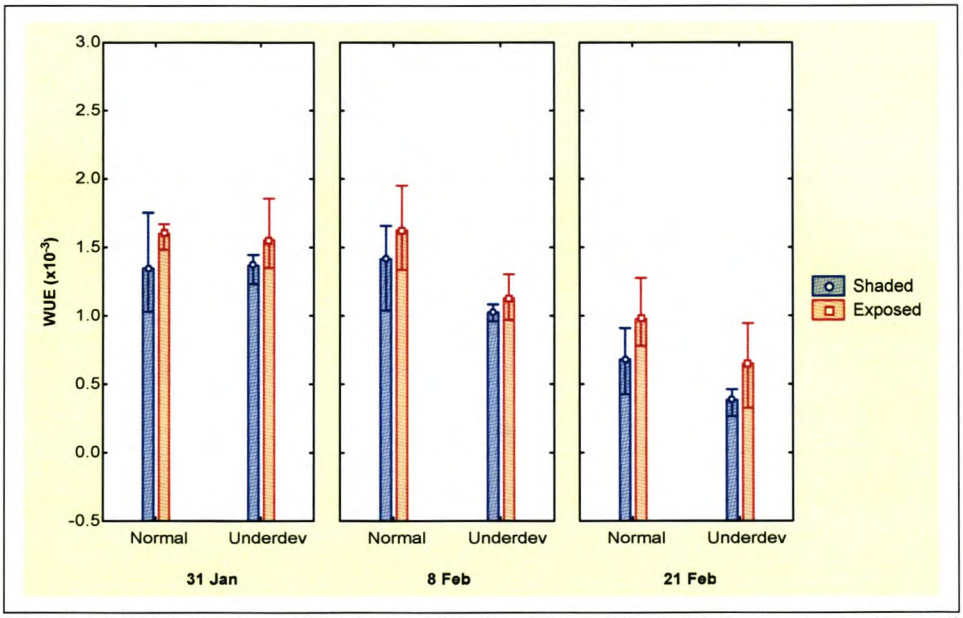

Figure 18 Water use efficiency (WUE) of basal leaves from normally and underdeveloped shoots in shaded and well-exposed canopies measured in the second, third and fifth week after véraison. Error bars indicate 95% confidence intervals (bootstrap analysis).

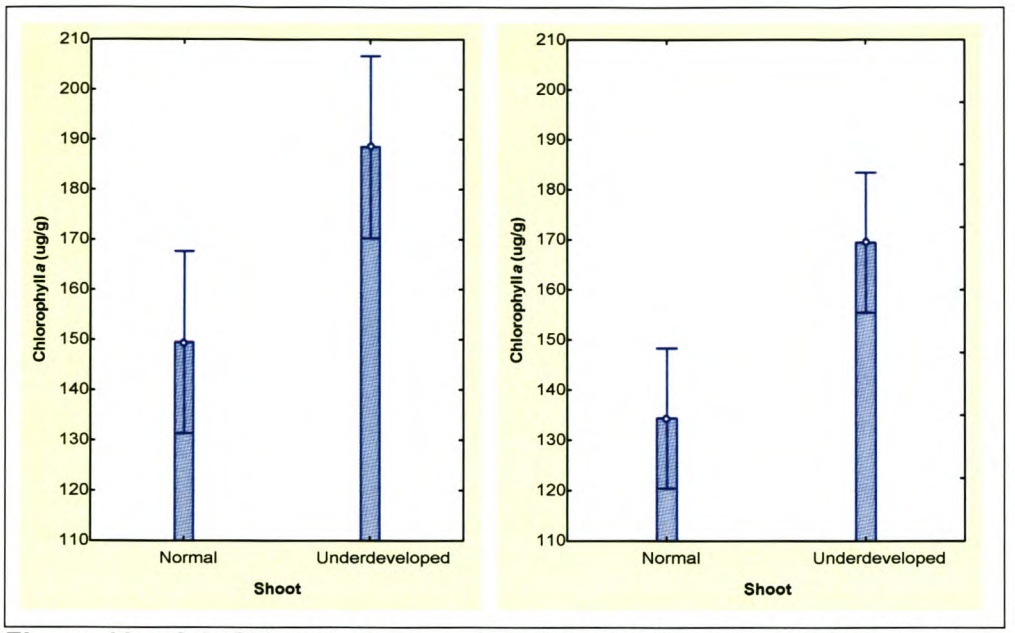

Figure 19 a & b Chlorophyll *a* concentration of primary leaves from normally and underdeveloped shoots measured five weeks after véraison. **a – 2002** ($p \leq 0.01$); **b – 2003** ($p \leq 0.01$). Error bars indicate 95% confidence intervals.

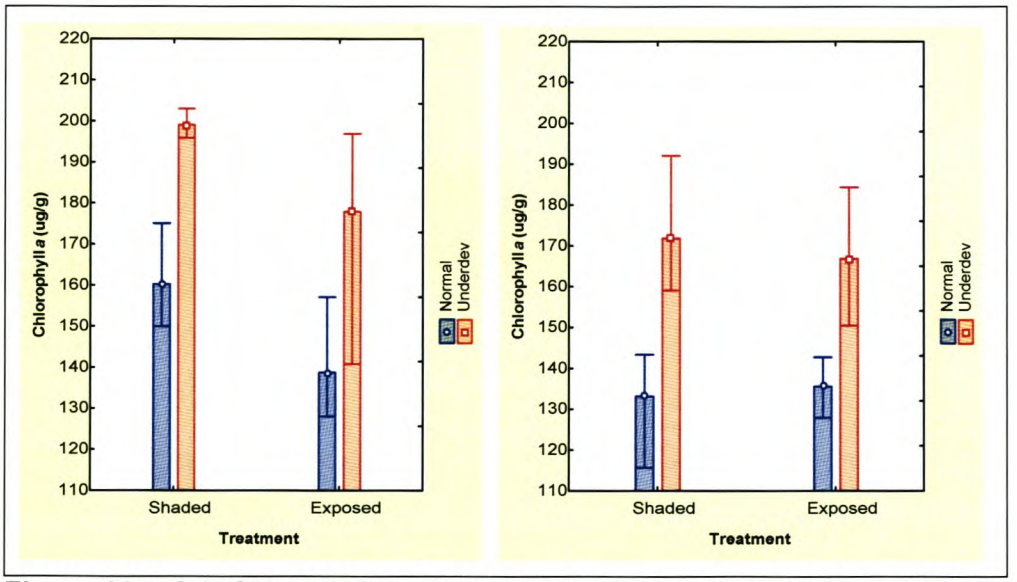

Figure 20 a & b Chlorophyll *a* concentration of primary leaves from normally and underdeveloped shoots in shaded and well-exposed canopies measured five weeks after véraison. **a – 2002**; **b – 2003**. Error bars indicate 95% confidence intervals (bootstrap analysis).

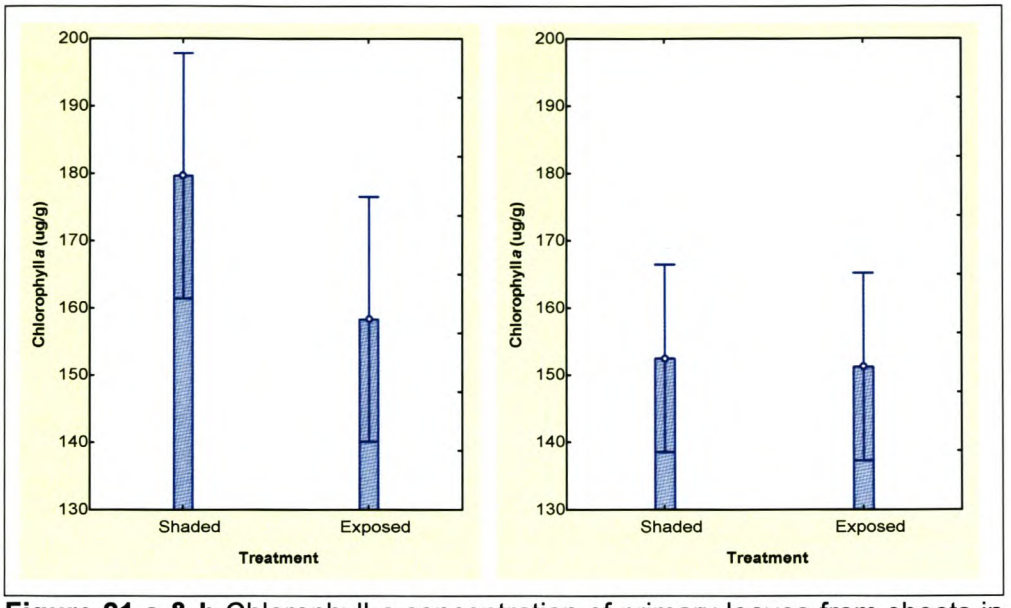

Figure 21 a & b Chlorophyll *a* concentration of primary leaves from shoots in shaded and well-exposed canopies measured five weeks after véraison. **a – 2002** ($p \leq 0.09$); **b – 2003**. Error bars indicate 95% confidence intervals.

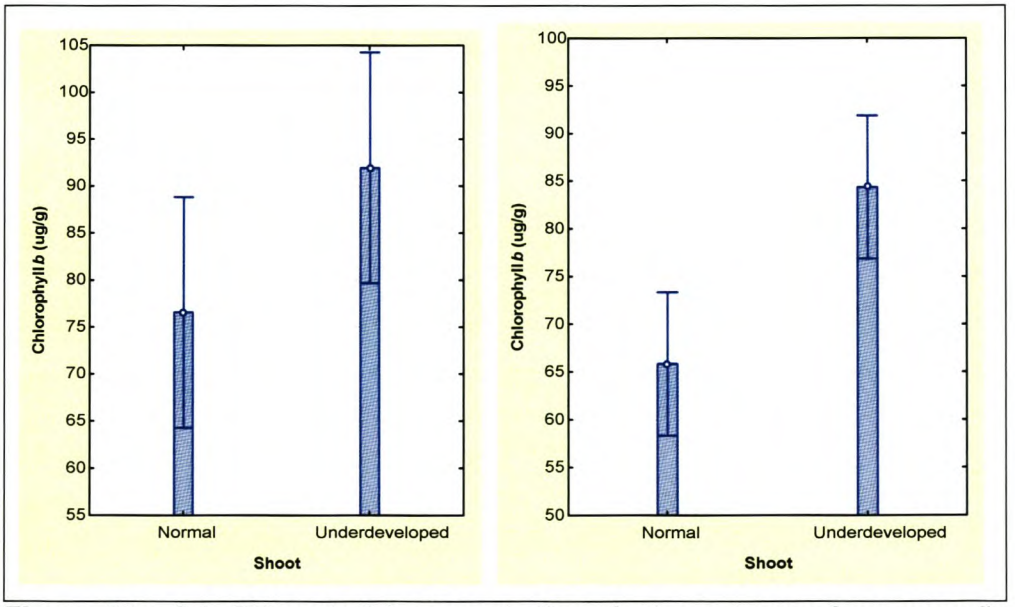

Figure 22 a & b Chlorophyll *b* concentration of primary leaves from normally and underdeveloped shoots measured five weeks after véraison. **a – 2002** ($p \leq 0.07$); **b – 2003** ($p \leq 0.01$). Error bars indicate 95% confidence intervals.

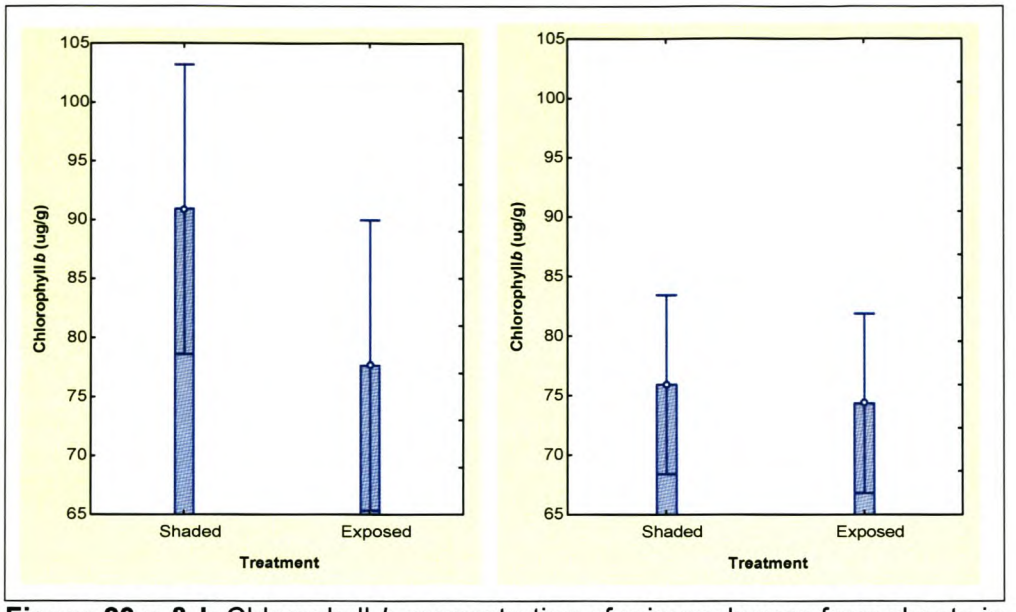

Figure 23 a & b Chlorophyll *b* concentration of primary leaves from shoots in shaded and well-exposed canopies measured five weeks after véraison. **a – 2002** ($p \leq 0.11$); **b – 2003**. Error bars indicate 95% confidence intervals.

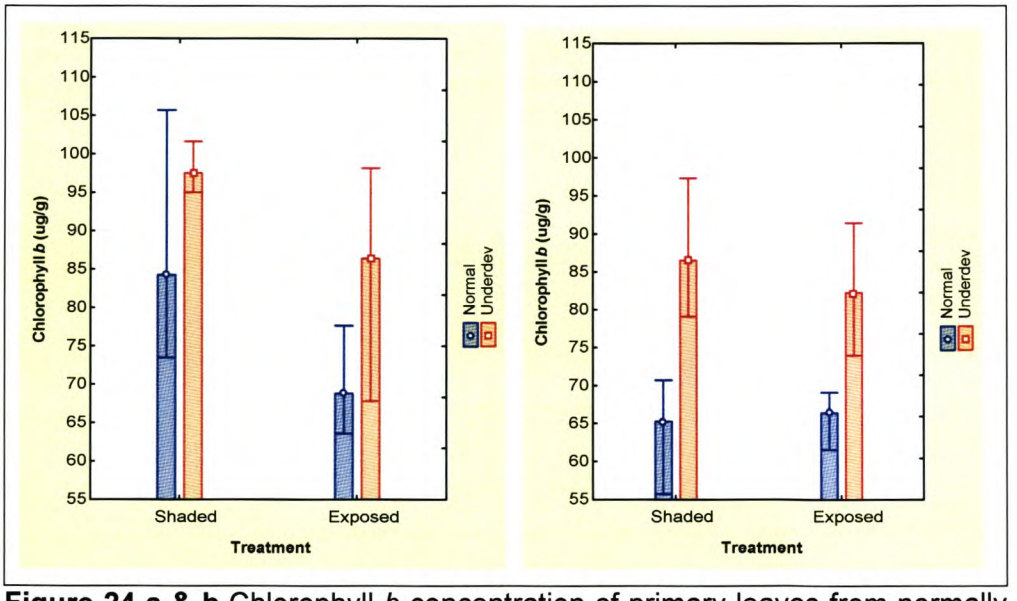

Figure 24 a & b Chlorophyll *b* concentration of primary leaves from normally and underdeveloped shoots in shaded and well-exposed canopies measured five weeks after véraison. **a – 2002**; **b – 2003**. Error bars indicate 95% confidence intervals (bootstrap analysis).

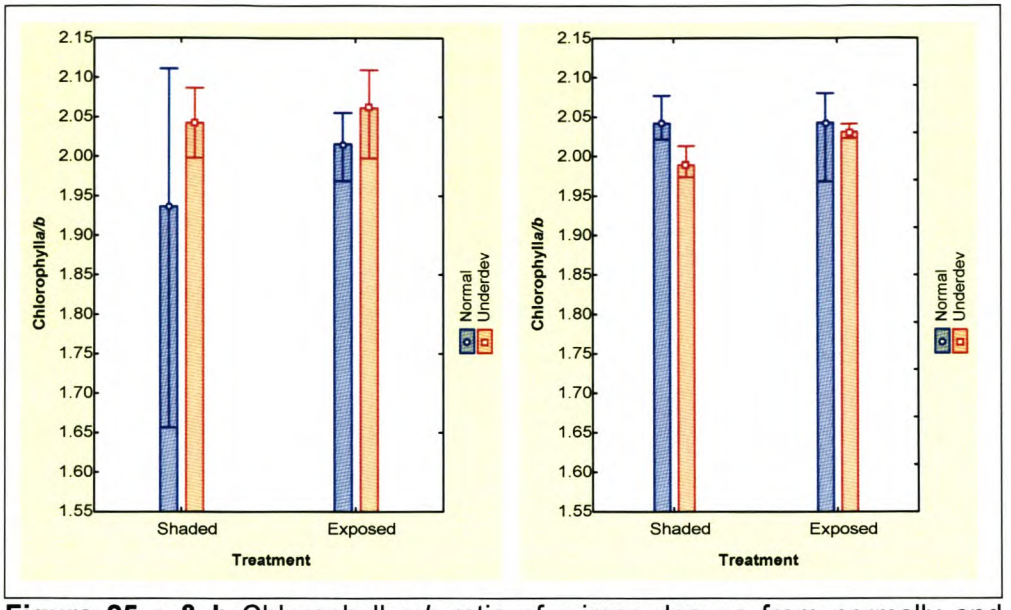

Figure 25 a & b Chlorophyll *a:b* ratio of primary leaves from normally and underdeveloped shoots in shaded and well-exposed canopies measured five weeks after véraison. **a – 2002**; **b – 2003**. Error bars indicate 95% confidence intervals (bootstrap analysis).

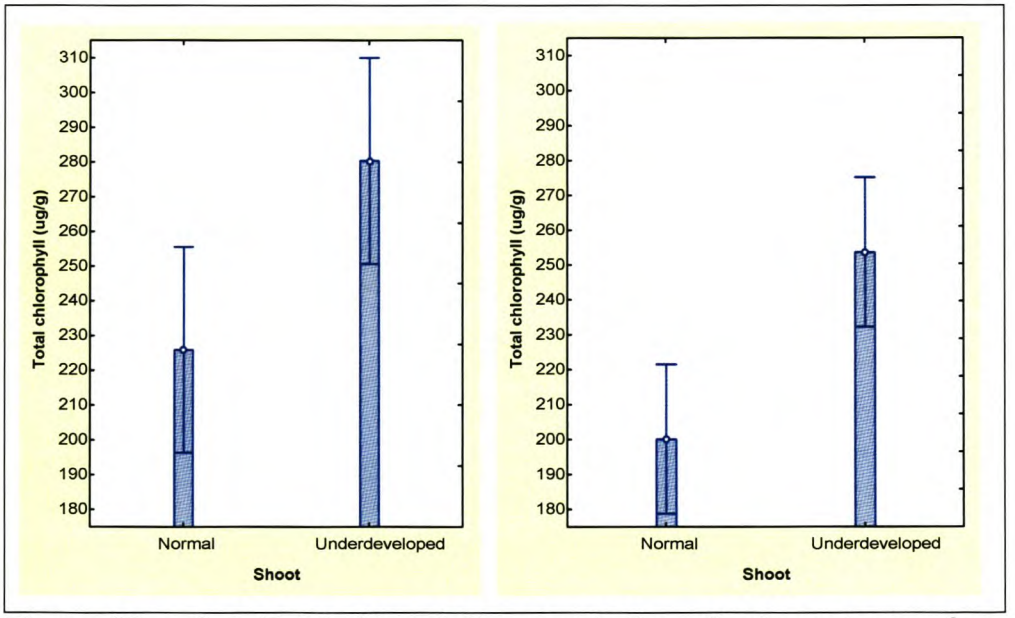

Figure 26 a & b Total chlorophyll concentration of primary leaves from normally and underdeveloped shoots measured five weeks after véraison. **a – 2002** ($p \leq 0.02$); **b – 2003** ($p \leq 0.01$). Error bars indicate 95% confidence intervals.

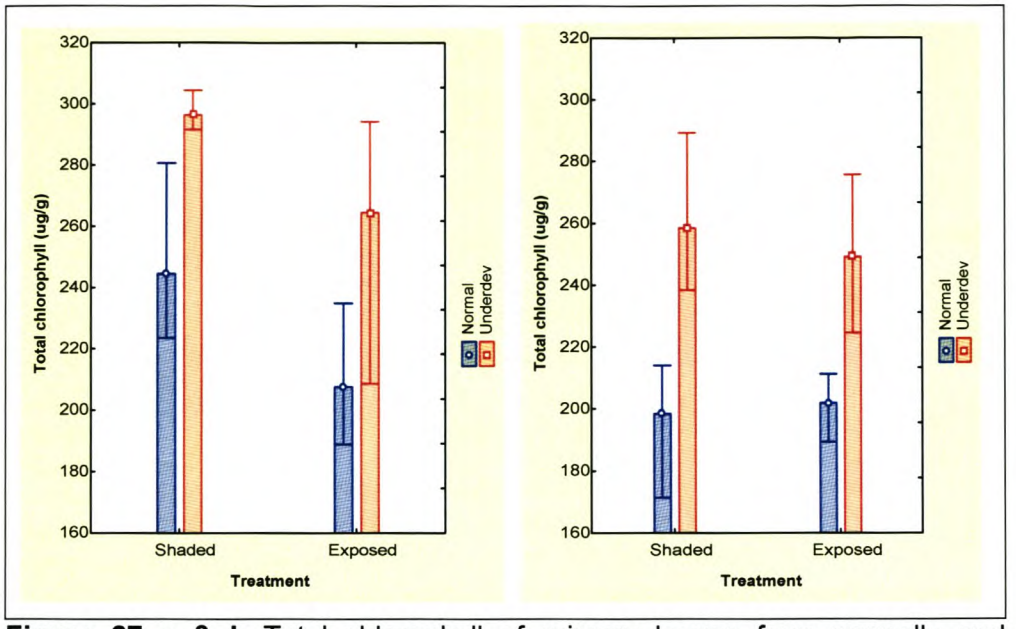

Figure 27 a & b Total chlorophyll of primary leaves from normally and underdeveloped shoots in shaded and well-exposed canopies measured five weeks after véraison. **a – 2002**; **b – 2003**. Error bars indicate 95% confidence intervals (bootstrap analysis).

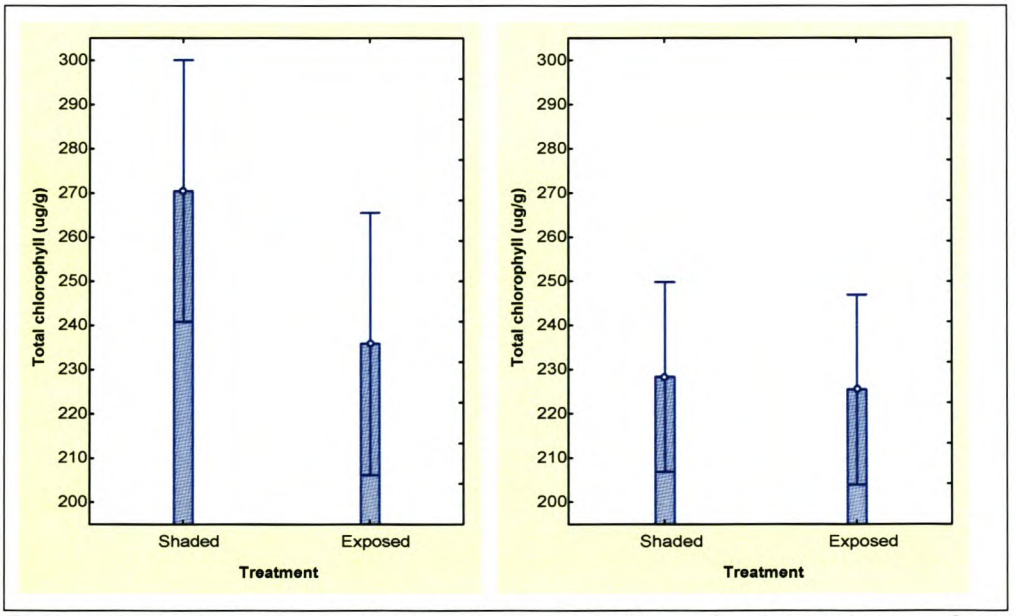

Figure 28 a & b Total chlorophyll concentration of primary leaves from shoots in shaded and well-exposed canopies measured five weeks after véraison. **a – 2002** ($p \leq 0.09$); **b – 2003**. Error bars indicate 95% confidence intervals.

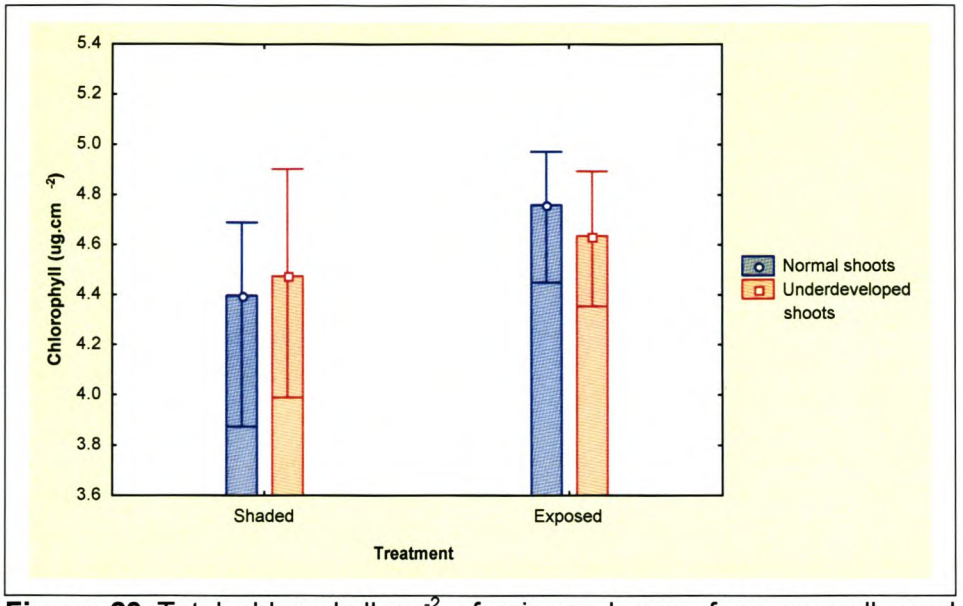

Figure 29 Total chlorophyll.cm^{-2} of primary leaves from normally and underdeveloped shoots in shaded and well-exposed canopies measured five weeks after véraison in **2003**. Error bars indicate 95% confidence intervals (bootstrap analysis).

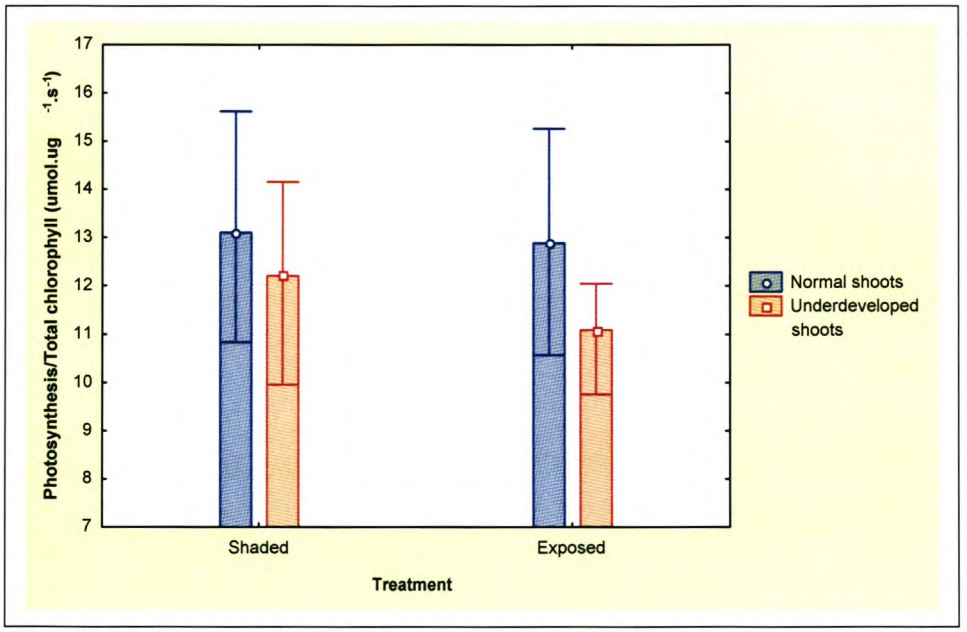

Figure 30 Photosynthetic rates per ug of chlorophyll of primary leaves from normally and underdeveloped shoots in shaded and well-exposed canopies measured five weeks after véraison in **2003**. Error bars indicate 95% confidence intervals (bootstrap analysis).

5. DISCUSSION

Photosynthetic parameters

Second week after véraison: No significant difference was found for any of the physiological parameters between normally and underdeveloped shoots in the second week after véraison. The level of PPFD received, as well as the photosynthetic and transpiration rates were similar. No external factor seemed limiting to the activity of the leaves, while internal factors, such as leaf age (Hunter & Visser, 1988) and internal resistance against CO_2 transfer (Kriedemann *et al.*, 1970), did not seem to play a significant role as yet.

It seemed as if the degree of canopy exposure affected the physiological activity of the leaves already in this early stage of grape ripening. A slightly higher WUE (albeit non-significant) was calculated for exposed canopies due to a somewhat higher photosynthetic rate and lower rate of transpiration. Factors such as the level of PPFD received and the internal CO_2 levels in the leaves could have affected these processes, although no statistically significant differences for these parameters were found between the shaded and well-exposed canopies.

Although the physiological activity per leaf area did not differ significantly between normally and underdeveloped shoots at this stage, it must be kept in mind that the primary leaves from the normally developed shoots were found to be much larger than those from the underdeveloped shoots (Chapter 3). Furthermore, a significantly higher number of secondary leaves with larger average areas were found on the normally developed shoots, resulting in a significantly higher total leaf area per shoot compared to underdeveloped shoots (Chapter 3).

The degree of canopy exposure did not seem to have a noticeable effect on the leaf number and size. However, the primary and secondary leaves in the shaded canopies tended to have a larger average area. The total leaf area per shoot was higher in shaded canopies, due to a somewhat higher number and higher area of the primary leaves (Chapter 3).

It was also found that the primary and secondary leaves from the normally developed shoots and from well-exposed canopies had a lower leaf area:mass ratio (i.e. thicker leaves) than those from the underdeveloped shoots and shaded canopies. It could well be expected that the anatomy of these leaves will also

differ, as Crookson *et al.* (1975) noted (according to Marini & Marini, 1983) a reduced differentiation of palisade and mesophyll cells in shade-grown leaves. Kappel & Flore (1983) also considered leaf morphology, chloroplast structure and mesophyll resistance as possible limiting factors to photosynthesis in light-stressed peach leaves. The above-mentioned factors may explain the higher WUE calculated for the exposed canopies, as the reduced differentiation of internal leaf tissues was linked with the decreased net photosynthesis measured (Marini & Marini, 1983).

The total production of carbohydrates was probably higher in the normally developed shoots compared to the underdeveloped shoots in the second week after véraison. Similar photosynthetic rates per leaf area were measured, whereas the normally developed shoots had a significantly higher total leaf area per shoot.

Since a higher total leaf area was measured on both types of shoots from shaded compared to exposed canopies, and no statistical difference was found for the photosynthetic rate per leaf area or the level of PPFD received, it could possibly be deduced that shoots from shaded canopies will produce higher levels of carbohydrates on a per shoots basis than shoots from exposed canopies. However, this may not be realized in practice, as the leaves in the shaded canopies had a higher leaf area:mass ratio and therefore thinner leaves with probable reduced differentiation of internal leaf tissues (Crookson *et al.*, 1975, according to Marini & Marini, 1983) than leaves from the exposed canopies. The above-mentioned factors may have had an equalising effect and it is therefore not easy to compare the total physiological productivity of the leaves from shaded and well-exposed canopies without any additional measurements.

Third week after véraison: In the third week after véraison significantly lower levels of PPFD were measured in the basal part of the canopies than in the previous week. Marini & Marini (1983) also found a decrease in the PPFD penetrating the canopy as the season advanced. This was attributed to normal shoot elongation. No increases in the shoot lengths, leaf number or area were, however, found in this study after véraison (Chapter 3). The decreased PPFD could therefore not have been due to self-shading in the canopies. As all the measurements were taken at the same time in the morning (10:00), the difference in the PPFD penetration in the canopy at this specific time could

possibly have been due to a change in the angle of sunlight penetration into the canopies as the season progressed.

Even though the amount of PPFD decreased, no significant change in the stomatal conductance, rate of transpiration or photosynthetic activity of the leaves from normally developed shoots was found. The internal CO_2 levels did not increase, while the WUE remained the same. The lower PPFD, and also other environmental effects such as moisture, temperature or gaseous conditions (Kriedemann, 1977) (not measured), therefore did not have a limiting effect on the physiological activity of the normal shoots. Compared to that, the stomatal conductance, rate of transpiration and photosynthesis decreased significantly in underdeveloped shoots. Increased internal CO_2 levels in the leaves were noticeable, while the WUE was significantly lower than that of the previous week.

Although the level of PPFD received by the underdeveloped shoots was lower than that received by the normally developed shoots, the average PPFD measured for the underdeveloped shoots was even in the shaded canopies still higher than a 1000 $\mu mol.m^{-2}.s^{-1}$. Since 704 – 1100 $\mu mol.m^{-2}.s^{-1}$ is considered to be optimum for the photosynthetic process (Champagnol, 1984), the level of PPFD was more than sufficient for maximal photosynthesis by the basal leaves from underdeveloped shoots and could thus not have been the reason for the significant decrease in physiological activity.

However, a higher degree of variation in the level of sunlight received by the basal leaves of underdeveloped shoots compared to that received by the leaves of normal shoots was measured in both the shaded and exposed canopies. Although the absolute levels of radiation measured is theoretically not inhibitive to the rate of photosynthesis, it could well be expected that there will be more variation in some of the other light dependent physiological processes in the leaves of the underdeveloped shoots compared to those of the normal shoots. Since the quality of a cluster is directly proportional to the physiological output of its shoot (Archer, 2001), it stands to reason that a larger variation in the grape quality from underdeveloped shoots could be expected, compared with the more homogeneous yield from normally developed shoots.

Temperature, amongst others, is a critical external factor affecting photosynthesis of the leaves (Kriedemann, 1977). No difference in the leaf temperature between normally and underdeveloped shoots was noticed (data not

shown). Therefore, although lower rates of transpiration were measured on underdeveloped shoots, transpiration was still efficient enough to maintain internal leaf temperature of the underdeveloped shoots. Too high leaf temperatures were thus probably not the reason for the lower photosynthetic activity measured in the leaves of the underdeveloped shoots.

Since the decrease in photosynthetic activity of the leaves from underdeveloped shoots cannot be satisfactory explained by external factors such as light or temperature, internal factors were also considered. A significantly lower ratio of total leaf area per gram grape berries was calculated for underdeveloped shoots compared to normally developed shoots (Chapter 6). According to Kriedemann (1977) and Hunter (1991) the photosynthetic activity of a leaf is dependent on the sink demand for assimilates and could thus increase the rate of photosynthesis as the demand for photosynthetates increased. However, the average leaf area per gram fresh berry mass for underdeveloped shoots was calculated as 10 cm^2 (Chapter 6). It is accepted that 10 – 12 $cm^2.g^{-1}$ fresh berry mass is generally required to ripen one gram of fruit (Hunter & Visser, 1990, and references therein). Therefore, even if the photosynthetic activity of the leaves on underdeveloped shoots was increased due to the high sink demand, the active leaf area probably was insufficient to ripen the clusters optimally.

This imbalance between vegetative and reproductive growth in underdeveloped shoots does not explain the increase in internal CO_2 levels found in the leaves. It rather seems as if the rate at which assimilates were utilised or stored was less than that at which it was supplied by the source tissues. This may have resulted in an inhibition of photosynthetic activity. As under-cropping is not a viable option (a low vegetative to reproductive growth ratio had been established), it stands to reason that there possibly also existed a physical reason for the decreased photosynthetic activity of underdeveloped shoots.

According to Kriedemann (1977), old leaves showed a reduction in both photosynthetic capacity and efficiency, which was associated with a substantial increase in internal resistance to CO_2 assimilation rather than a decrease in stomatal conductivity. There is, however, no reason to believe that the basal leaves from underdeveloped shoots differed significantly in age compared to the leaves of normal shoots. Thus the decreased photosynthetic rate measured on underdeveloped shoots was probably not due to leaf ageing.

Marini & Marini (1983) linked reduced net photosynthesis with poorly differentiated palisade and mesophyll cells in peach leaves. It is possible that the internal structure of leaves from normally and underdeveloped shoots differed from each other. Unfortunately, no anatomical studies of the basal leaves were done. According to the same source, Crookston *et al.* (1975) found increased mesophyll resistance in shade-grown bean leaves. Shading of leaves (including grape leaves) may possibly induce a similar result. As lower PPFD (albeit non-significant) was measured for underdeveloped shoots and shoots in the shaded canopies, the decreased photosynthetic rate could have been due to a slightly lower mesophyll conductance compared to normally developed shoots and shoots from exposed canopies.

Since higher rates of photosynthesis per leaf area (Figs. 4 & 6) as well as higher total leaf area per shoot (Chapter 3) were measured for normal shoots compared to underdeveloped shoots, it may be assumed that the total production of carbohydrates is higher in the normally developed shoots.

Although the sunlight penetration in the basal parts of shaded canopies decreased significantly from two to three weeks after véraison, the changes in the measured physiological parameters, except for transpiration and maybe photosynthesis, were non-significant. The patterns that were visible in the second week, continued in the third week after véraison. The leaves in the well-exposed canopies displayed non-significantly higher levels of transpiration and photosynthetic rates, as well as higher WUE ratios and stomatal conductance than leaves in shaded canopies. Lower levels of internal CO_2 were also measured in the exposed canopies. Albeit not statistically significant, the beneficial effect of better leaf exposure on the physiological activity of the well-exposed canopies could clearly be seen from the data.

Interestingly, except for the PPFD, larger differences in the physiological parameters were found between the normal and underdeveloped shoots in the well-exposed canopies. Maybe some factor other than the immediate radiation received is responsible for the difference in activity between the normally and underdeveloped shoots. Since canopy management practices (and thus the creation of well-exposed canopies) are strongly recommended and executed in the vast majority of commercial vineyards, the importance of homogeneous, normally developed shoots in the canopy is once again illustrated.

Fifth week after véraison: As the season progressed by a further two weeks, the level of sunlight received by the basal leaves decreased even further. This is in accordance with Hunter & Visser (1989) who found a decrease in the PPFD of the cluster and basal leaves from véraison to ripeness. The further decrease in the PPFD could once again be ascribed to the decrease in the angle of sunlight penetration with respect to the canopies.

A sharper decrease was found for the underdeveloped compared to the normal shoots, while no significant difference was found between the underdeveloped shoots from well-exposed and shaded canopies. Smart (1988) found a large number of underdeveloped shoots in canopy interiors, which will most certainly affect the sunlight penetration to the basal parts of shoots. The significantly lower levels of PPFD received by the underdeveloped shoots compared to the normal shoots in both the shaded and exposed canopies could thus possibly be explained by the development of underdeveloped shoots in the interiors of shaded as well as exposed canopies. Another probable explanation for the lower PPFD received by the underdeveloped shoots, is that these shoots could have been overlooked during shoot positioning and thus pushed to the canopy interior to make room for the normally developed shoots. The latter could then be responsible for the overshadowing of the underdeveloped shoots due to their thicker shoots and larger leaves.

From the third to the fifth week after véraison the photosynthetic rates of the normally and underdeveloped shoots as well as the rates in the shaded and exposed canopies decreased significantly. This is in accordance with Kriedemann *et al.* (1970), who found a decline in photosynthesis after a leaf reaches its mature size. Since only basal leaves were measured in this experiment, all of them attained their full mature size before véraison commenced (Chapter 3) and the observed decrease in photosynthetic rate was well expected.

Leaf photosynthesis depended upon the demand for assimilates (Hunter *et al.*, 1991), as it was found that an increase in the demand for photosynthetic products resulted in an increased photosynthetic activity. According to Kriedemann (1977) the demand for photosynthetate by sinks had a downward trend as the season advanced, which accounts for the findings of Hunter *et al.* (1994) that the photosynthetic activity of all the leaves, regardless the leaf position, decreased as the season advanced. This could also be a possible

explanation for the significant decrease in photosynthetic activity from three to five weeks after véraison.

Five weeks after véraison the air temperature was 35-36°C, compared to the 31-32°C two weeks earlier (data not shown). The temperature of both days was higher than the optimum of 25°C for photosynthesis (Kriedemann, 1977). The effect of water stress and tissue desiccation together with the high temperature on the photosynthetic rate would have been more significant five weeks after véraison (micro-irrigation was applied one week after véraison).

Therefore, the significant decrease in the photosynthetic rate from three to five weeks after véraison could be ascribed to the leaf age, the decrease in sink strength as the season advanced, decreased PPFD received by the basal leaves, as well as the inhibitory effect of possible leaf dehydration with high internal leaf temperatures.

The internal CO_2 levels in the leaves increased from the third to the fifth week after véraison. This may be an indication of decreased sink strengths as the season progressed, resulting in a decrease in assimilate transport and an accumulation of CO_2 in the leaves together with an increased resistance to CO_2 assimilation with an increase in leaf age (Kriedemann, 1977).

The decrease in stomatal conductivity as the season progressed is in accordance with the findings of Hunter & Visser (1988) and Archer & Strauss (1989b). This decrease, as well as the corresponding decrease in transpiration rate, was ascribed to a gradual increase in water stress. Since irrigation was only applied two weeks before pea size berry and one week after véraison during the course of this experiment, the increased water stress as the season advanced could have been a strong factor affecting the stomatal conductance and transpiration. It was found that as water stress developed in vines due to soil water depletion, stomatal conductance decreased before any change in the leaf water potential was detected (Flexas *et al.*, 2000), due to the root signal (mainly abscisic acid) that regulates stomatal aperture under such conditions (Davies & Zhang, 1991). The water stress would also have reduced the photosynthetic rate, since according to Archer & Strauss (1989b), Bravdo *et al.* (1972) found that the rate of photosynthesis declined with increasing water stress.

Water loss from the leaves, measured as the rate of transpiration in the fifth week after véraison, was higher than would have been expected from the stomatal conductance. It is possibly explained by the high temperatures of 35-36°C measured on that specific day (data not shown). At elevated temperatures the vapour pressure gradient between the leaf and air is further accentuated, which leads to high transpiration loss even though the stomata are closed (Kriedemann, 1977). Under stress conditions, functional processes are therefore not necessarily coordinated.

The WUE ratio of the normal and underdeveloped shoots in shaded and exposed canopies decreased significantly between the third and fifth week after véraison, due to the decrease in photosynthesis relatively to the transpiration rate. According to Schultz (1997), Grimes & Williams (1990) and Williams *et al.* (1994) have shown than the WUE ratio increased substantially with decreasing water supply. It was probably due to the decrease in stomatal conductivity, since the stomatal closure is the dominant factor changing WUE during water deficit (Schultz, 1997). Since the final micro-irrigation was applied one week after véraison, it may be assumed that at least moderate water stress was experienced five weeks after véraison. The decreased WUE found is thus contrary to the findings of Grimes & Williams (1990) and Williams *et al.* (1994).

It should, however, be kept in mind that the water loss (rate of transpiration) was higher than would have been expected from the stomatal conductance due to the very high temperature five weeks after véraison. Despite the low stomatal conductivity, the high transpiration rate would have masked any possible increase in WUE due to stomatal closure. It is therefore possible that if the measurements were taken on a cooler day in the same week, the WUE may have showed an increase as the literature suggests.

Leaves from underdeveloped shoots displayed lower levels of physiological activity than those from normal shoots in shaded and exposed canopies and this may possibly be explained by the lower PPFD levels received by the leaves or the lower total leaf area per gram fresh berry mass.

The PPFD levels measured with the normally developed shoots never decreased below 1000 $\mu mol.m^{-2}.s^{-1}$, while the average levels received by the underdeveloped shoots were below or very close to 700 $\mu mol.m^{-2}.s^{-1}$ in the shaded and exposed canopies. Since 700 $\mu mol.m^{-2}.s^{-1}$ is considered to be the

minimum intensity where the photosynthetic process can proceed at an optimal level (Champagnol, 1984), it may be possible that the diminishing light exposure of the basal leaves on the underdeveloped shoots inhibited the activity of these leaves.

The decreased photosynthetic rate could possibly have caused the internal CO_2 levels in the leaves to increase, with the resultant closure of stomata and decrease in stomatal conductivity and transpiration. The ageing leaf anatomy and possible increasing internal resistance against CO_2 transfer could also have had an effect on the above-mentioned physiological processes.

Higher PPFD levels, stomatal conductivity and photosynthetic and transpiration rates as well as WUE ratios were measured in the exposed compared to the shaded canopies. These findings are in accordance with those of Hunter & Visser (1988) who found an increase in sunlight penetration, an increase in photosynthetic and transpiration rates and a decreased stomatal resistance with increased degrees of canopy defoliation. The higher WUE ratio calculated in the exposed canopies is also in accordance with the findings of Hunter & Visser (1988), who suggested a possible more effective utilization of CO_2 in the more exposed canopies. Archer (1988) also stated that during optimal light conditions, leaves receiving direct sunlight were photosynthetically the most effective, and the more the leaves were exposed to PPFD the higher the rate of photosynthesis.

Chlorophyll (five weeks after véraison):
Higher chlorophyll *a*, chlorophyll *b* and total chlorophyll concentrations ($\mu g.g^{-1}$ fresh mass) were found in leaves from underdeveloped shoots compared to normal shoots in both years of study. Since a large percentage of underdeveloped shoots generally occur in the canopy interior (Smart, 1988) and higher chlorophyll concentrations were found in leaves under shaded conditions (Kappel & Flore, 1983), the low light intensities may have resulted in the high chlorophyll levels in the leaves on underdeveloped shoots.

In 2002 it seemed as if the degree of canopy exposure affected the chlorophyll levels, since higher chlorophyll *a*, chlorophyll *b* and total chlorophyll ($\mu g.g^{-1}$) were found in the leaves from the shaded canopies. The chlorophyll *a:b* ratio was unaffected. In 2003 no such differences between the canopies were found, except for the chlorophyll *a:b* ratio. In the shaded canopies this ratio was

significantly higher in the leaves from the normally compared to the underdeveloped shoots, while in the case of the underdeveloped shoots significant higher ratios were calculated in the exposed compared to the shaded canopies. According to Hunter & Visser (1989), Sestak (1966) stated that chlorophyll *a* is considered a more exact characteristic of photosynthetic activity. It may therefore be stated that normally developed shoots and well-exposed canopies are extremely important for expression of the main light absorbing pigment and the attainment of optimal photosynthetic activity in the canopy.

A higher leaf area:mass ratio and lower leaf mass were found on underdeveloped compared to normally developed shoots. Since chlorophyll was determined on a per gram fresh leaf basis, a larger leaf area from the underdeveloped shoots were used for each analysis than from the normally developed shoots. As the effective leaf area (and not the mass) in the canopy is considered an indication of the physiological potential of the canopy (Carbonneau *et al.*, 1997), the chlorophyll content per unit leaf area was determined in 2003. No statistical significant difference was found between the normally and underdeveloped shoots. It may be reasoned that the light intercepting, and thus the physiological, potential per unit leaf area of the leaves from the normal and underdeveloped shoots was similar.

However, according to Hunter & Visser (1989) the light intercepting ability of a vine leaf is not necessarily closely related to the CO_2 assimilating ability. Therefore the assimilation number (μmol CO_2.μg chlorophyll^{-1}.s^{-1}) of the leaves from the different shoots was also calculated for 2003. Although not statistically significant, it seemed as if these levels were lower for underdeveloped shoots.

It may also be reasoned that the more chlorophyll that occurs in the leaf, the higher the total photosynthetic productivity of the leaf, since the highest photosynthetic activity was reached when the chlorophyll concentration (mg.dm^{-2}) reached its peak (Kriedemann *et al.*, 1970). Hunter & Visser (1989) found a significant relationship between the chlorophyll concentration (μg.g^{-1}) and photosynthetic activity for leaves in the canopy interior exposed to lower light conditions. As already discussed, the chlorophyll concentration (μg.g^{-1} fresh leaf mass) was higher in the leaves from the underdeveloped shoots, while the concentration expressed as μg.cm^{-2} leaf area did not differ significantly from that of leaves on normal shoots.

It was further found that the average area of leaves on underdeveloped shoots was significantly smaller than that on normal shoots, while significantly higher leaf area per shoot was measured for the normally developed shoots (Chapter 3). Although the assimilation number between the leaves did not differ significantly, significantly higher levels of total chlorophyll per leaf were found in the leaves on the normal shoots (data not shown). An equal amount of chlorophyll.cm^{-2} and non-significant difference in the assimilation number may lead to a higher production of photosynthetates in leaves on normally developed shoots compared to those on underdeveloped shoots, due to the larger leaf area on a per leaf and per shoot basis.

The non-significantly higher chlorophyll *a*, chlorophyll *b* and total chlorophyll contents ($\mu g.g^{-1}$) of leaves in shaded compared to well-exposed canopies are in accordance with the findings of Kappel & Flore (1983) who also found higher chlorophyll contents in leaves under shaded conditions. In 2003 the degree of canopy exposure hardly seemed to affect the chlorophyll concentration at all. Since it was found that leaves that developed in shaded canopies had a higher leaf area:mass ratio than those in exposed canopies (Chapter 3) and that the effective leaf area is an indication of the physiological potential of the canopy, the chlorophyll content per unit leaf area was determined for 2003. No significant difference between the shaded and well-exposed canopies was found. It rather seemed as if the leaves in the exposed canopies had a higher average chlorophyll.cm^{-2} than those in the shaded canopies, which could induce a better light intercepting ability of the leaves in exposed canopies. However, no statistically significant difference was found in assimilation number, calculated in 2003, between the leaves from the shaded and well-exposed canopies.

The chlorophyll concentration per unit leaf area and the assimilation number were not calculated for 2002. From the chlorophyll *a*, chlorophyll *b* and total chlorophyll data, it was concluded that the degree of canopy exposure had a larger effect on the chlorophyll concentration in 2002 than in 2003. Although no significant difference in chlorophyll per unit leaf area and the assimilation number between shaded and exposed canopies was found in 2003, the results probably would have been a little different in 2002.

The data collected over the two years indicated that the chlorophyll content per unit fresh leaf mass was higher in the leaves from the underdeveloped compared to the normal shoots. This may have been due to lower light intensities received

by the underdeveloped shoots, since the leaves that developed in the more shaded canopies tended to have higher chlorophyll per unit fresh leaf mass than those in the more exposed canopies Kappel & Flore, 1983; Marini & Marini 1983). However, the reaction to canopy treatments was not similar in the two years monitored. Interestingly, in the year where the degree of canopy exposure hardly seemed to affect the chlorophyll concentrations at all, the difference in chlorophyll content per unit fresh leaf mass was more apparent between the normally and underdeveloped shoots.

When the photosynthetic activity of the leaves from the normally and underdeveloped shoots was compared with the chlorophyll content ($\mu g.g^{-1}$), no positive relationship could be found. This is in accordance with Kriedemann *et al.* (1970) and Hunter & Visser (1989) who found no consistent relationship between the chlorophyll concentration and the photosynthetic activity of leaves.

Higher photosynthetic rates were measured in exposed than in shaded canopies, while leaves on normally developed shoots displayed higher rates of photosynthesis than those on underdeveloped shoots. This difference was particularly significant in shaded canopies. On the other hand, higher chlorophyll concentrations ($\mu g.g^{-1}$) were found in leaves on underdeveloped compared to normal shoots, while the chlorophyll concentration also tended to be higher in the shaded compared to the well-exposed canopies. The latter is in accordance with the findings and statements of Kappel & Flore (1983), Marini & Marini (1983) and Smart (1988). The difference in chlorophyll content of the different shoots was more pronounced in shaded canopies.

Therefore, based on measured photosynthetic activity, as well as the total assimilation per leaf or shoot as indicated by the assimilation number, canopy management practices inducing well-exposed canopies are very important, while homogeneous normal shoot development is of great importance, especially when a more shaded canopy is preferred in order to protect the clusters against very high temperatures, sunburn, and negative compositional changes.

6. CONCLUSIONS

In the first five weeks after véraison, photosynthesis, transpiration, stomatal conductivity and WUE decreased as berry ripening progressed, while the internal

CO_2 levels in the leaves increased. This was mainly ascribed to an increase in leaf age of the basal leaves and consequent change in internal anatomy and functionality, decreased demand for assimilates by the vine, decreased PPFD received and an increase in water deficit.

The improving effect on physiological activity induced by exposed canopies became apparent from the third week after véraison. Although none of the differences were statistically significant, leaves on shoots in well-exposed canopies received higher levels of PPFD, displayed higher rates of photosynthesis and transpiration with lower stomatal resistance and lower internal CO_2 levels. The photosynthetic activity of the normal shoots in the exposed canopies was significantly higher than their activity in the shaded canopies five weeks after véraison. The same applied to the underdeveloped shoots.

The difference in physiological activity between leaves from normally and underdeveloped shoots also became only apparent in the third week after véraison. Normal shoots displayed significantly higher rates of photosynthesis and transpiration than underdeveloped shoots in the third as well as the fifth week after véraison. Likely reasons are the lower source:sink ratio found on underdeveloped shoots as well as a possible physical resistance against gas transfer in the leaves on those shoots. Although not constantly significant, normal shoots further received higher PPFD levels, while higher stomatal conductance and lower internal CO_2 levels of the leaves were measured than in the case of underdeveloped shoots. A higher WUE ratio was also calculated for the normal shoots.

Even though the results were not statistically different, they underlined the importance of a well-exposed canopy and homogeneous, normally developed shoots to promote the physiological activity of the leaves. The results therefore confirm that canopy management practices contribute to the improvement of the functionality of leaves in canopies that are less than ideal.

As it was stated that physiological functioning of the canopy affects fruit composition and ultimate wine quality (Smart *et al.*, 1985), it could well be expected that the grape and wine quality from the exposed canopies will be better than that from the shaded canopies.

Higher levels of chlorophyll *a*, chlorophyll *b* and total chlorophyll ($\mu g.g^{-1}$) were found in leaves from underdeveloped than normally developed shoots. It is not clear how important the effect of canopy exposure is on the chlorophyll content of the leaves, since different results were obtained in two consecutive years. No positive correlation between the photosynthetic activity and the chlorophyll concentration of the leaves was found in 2002. The limiting values of chlorophyll with regard to optimal photosynthetic activity need to be clarified in further studies.

In 2003 the chlorophyll concentration per unit leaf area ($\mu g.cm^{-2}$) and the assimilation number ($\mu mol.\mu g^{-1}.s^{-1}$) were additionally calculated. Since no statistically significant differences between the normally and underdeveloped shoots or between the shaded and well-exposed canopies were found, it was concluded that the effective area per leaf or per shoot played a bigger role than chlorophyll concentration or activity in the differences in photosynthetic productivity of the leaves on normally and underdeveloped shoots in the shaded or well-exposed canopies.

It was found that the physiological activity (photosynthetic and transpirational rates) of leaves on normal shoots differed significantly from those on underdeveloped shoots on a leaf area basis. Since the total leaf area per normal shoot was also significantly higher than per underdeveloped shoot, it can be accepted that the total carbohydrate production of the normal shoots would have been significantly higher. According to Koblet (1977), the grape berries are the most important sinks for assimilates during the ripening period. It is therefore expected that the size and quality of the yield from normally developed shoots will be higher than that from underdeveloped shoots.

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CHAPTER 5

RESEARCH RESULTS

THE EFFECT OF SHOOT HETEROGENEITY ON THE DAY CYCLES OF CERTAIN PHYSIOLOGICAL PROCESSES OF SHIRAZ/RICHTER 99 GRAPEVINES

1. ABSTRACT

In this study, the physiology of normally and underdeveloped shoots was compared in an attempt to quantify the effect of shoot heterogeneity in a Shiraz/Richter 99 vineyard. The field trial was performed in the Stellenbosch area, Western Cape, South Africa. Comparisons based on the day cycles of certain physiological parameters were made between normally and underdeveloped shoots in shaded and well-exposed canopies. It was found that the most apparent differences in the physiological activity between normally and underdeveloped shoots in shaded and well-exposed canopies occurred from 10:00 to 14:00, the most significant being at 12:00. The activity of the shoots in the exposed canopies peaked at 12:00, compared to 10:00 in the shaded canopies. The improving effects of canopy management practices on the physiological activity of leaves were well illustrated. Higher maximum levels of PPFD (with more uniform light penetration), photosynthesis, transpiration and stomatal conductance were measured in the exposed than in shaded canopies between late morning and early afternoon. Higher stomatal conductance and transpiration rates and significantly higher rates of photosynthesis were measured for normally compared to underdeveloped shoots, with higher WUE ratios calculated between 10:00 and 14:00. Canopy management practices to improve canopy microclimate and induce homogeneous, normally developed shoots are once again strongly recommended for the production of top quality grapes.

2. INTRODUCTION

It is essential for the vine producer to maximise yield without impairing grape quality or the longevity of the vine. According to Carbonneau (1995) the yield, berry ripening and thus the ultimate wine quality depend on the canopy structure. The exposed leaf area that was able to reach their photosynthetic potential was a good indication of the physiological potential of the canopy (Carbonneau *et al.*, 1997). This statement can possibly be altered so that the leaf area on a shoot that is able to reach its photosynthetic potential is a good estimation of the physiological potential of that shoot and thus also the size and quality of its clusters.

Experiments on the source:sink ratio in canopies indicated that all leaves had the potential to photosynthesise at a higher rate than that which is actually measured under field conditions (Hunter *et al.*, 1994, and references therein). Although genetic factors set an upper limit to photosynthetic capacity, observed instantaneous rates of photosynthesis are more commonly dictated by environmental conditions and internal control mechanisms that affect overall demand for photosynthetates and partitioning of assimilates within the vine (Huglin, 1972, according to Kriedemann, 1977). The leaf area in relation to crop load is amongst the factors mentioned by Petrie *et al.* (2000) affecting the photosynthetic rate of individual leaves.

The efficiency of the leaves was dependent on the amount and intensity of sunlight interception (Hunter, 1991). The more the leaves were exposed to PPFD, the higher the rate of photosynthesis up to a certain point (Archer, 1988), while increased shading led to a decrease in the photosynthetic rate per unit leaf area (Kappel & Flore, 1983; Caspari & Lang, 1996). Individual leaves should thus be exposed in such a way that photosynthetic conditions can be optimal for each leaf (Hunter *et al.*, 1991).

According to Smart (1987), a linear relationship exists between radiation and temperature, since radiation increased the temperature of the exposed leaves and resulted in an increase in photosynthetic activity. Excessive temperatures will however decrease photosynthetic activity, mainly due to water deficiency and leaf tissue desiccation (Kriedemann, 1977).

Since the CO_2 used during photosynthesis is assimilated through the open stomata, a strong relationship between stomatal conductance and photosynthetic activity should exist. However, water loss through transpiration occurs at the same time than CO_2 uptake and, in order to prevent excessive water loss, stomata will close (and photosynthesis inhibited) when the water supply becomes limiting (Kriedemann, 1977). Under conditions of extreme temperatures, water loss through the leaf can still occur due to the accentuated vapour pressure gradient, even though the stomata are closed (Schultz, 1997). As a result, the leaf water potential will decrease, which indicates that there is not necessarily a constant relationship between leaf water potential and stomatal conductance.

For many years it has been generally accepted that as the soil dries, water uptake is reduced with the resultant decrease in the leaf water status, increase in ABA concentration and closure of the stomata (Davies & Zhang, 1991; Düring *et*

al., 1996). Still, it has often been noticed that a decrease in stomatal conductance preceded changes in leaf water potential (Düring *et al.*, 1996, and references therein). According to findings quoted by Davies & Zhang (1991), the ABA produced by the root tips when sensing water deficiency in the soil is transported through the xylem vessels in the transpiration stream to the shoots where conductance is impaired due to the induced closure of the stomata by the ABA.

According to Düring *et al.* (1996), Tardieu & Davies (1993) suggested that stomatal sensitivity to the ABA signal from the roots increases as the leaf water potential declines. Correira *et al.* (1995), as quoted by Düring *et al.* (1996), found that the stomatal conductance was lower in the afternoon than in the morning for any given concentration of ABA. However, no significant decrease in the bulk leaf water potential was apparently found and it was therefore assumed that a localized increase in sensitivity to ABA occurred in the leaves.

According to research quoted by Davies & Zhang (1991), the reasonable correlation found between xylem ABA and stomatal resistance could be the reason why diurnal variation in stomatal conductance was related to the diurnal variation in xylem ABA concentration. However, root signalling had been regarded as an early warning system that induce adaptation processes before the water status of the vine declines (Düring *et al.*, 1996). At severe soil water deficiency levels, stomatal conductance is apparently determined by other factors such as ABA production by the leaves (Davies & Zhang, 1991; Düring *et al.*, 1996).

A lot of studies have already been done on the various relationships between the soil water content, leaf water potential, stomatal conductance, rate of transpiration and CO_2 assimilation rate. In short, there seems to exist a stronger correlation between the stem water potential and the available soil water content (Naor, 1998), the vine water status (Bravdo & Naor, 1995) and the stomatal conductance (Davies & Zhang, 1991; Bravdo & Naor, 1995; Naor & Bravdo, 1996; Naor, 1998) than between the leaf water potential and the above parameters. Only the predawn measurement of leaf water potential seemed to correspond with soil water content (Archer & Strauss, 1989). According to Deloire (2003, personal communication) predawn leaf water potential quantifies the hydric status of the vine in direct relation to the soil water that is accessible to the roots. The predawn leaf water potential also proved to be useful as an indicator of photosynthetic activity of field-grown vines under stress conditions

(Lopes, 1999), since a strong correlation was found with net assimilation rate and stomatal conductance under these conditions.

Davies & Zhang (1991) introduced the concept of stomatal control by the soil water status *via* root signals; hence stomatal conductivity is not directly affected by the plant water status (Naor & Bravdo, 1996). Research quoted by the latter source clearly showed that stomatal conductance is better correlated with soil water availability than with leaf water potential. Earlier literature, such as Kriedemann (1977), however stated that if evaporative demand of the leaf environment caused the transpiration rate to exceed that of the water supply, the increased moisture stress which will develop inside the leaves would induce complete closure of the stomata. Smart (1974) found the critical value of leaf water potential that induces stomatal closure to be around –1,3 MPa.

It is not very clear from the literature how the effects of the atmospheric conditions and soil water supply on stomatal conductance are combined inside the grapevine. According to the results of Naor & Bravdo (1996), stomatal conductance only responded to atmospheric water stress when the soil water availability was low. In almost direct contrast, Lopes (1999) stated that due to the absence of a root signal, the stomatal conductance was mainly dependent on atmospheric conditions in wet soil. They further stated that combined effects of high light intensity, high temperatures and vapour pressure deficits can override the effects of leaf water status on diurnal fluctuations of net CO_2 assimilation (and thus photosynthesis), especially when the vines are well supplied with water. The research done by Schultz (1996; 1997) indicated differences in the way grapevine cultivars combat water stress conditions. Significant differences between Grenache and Shiraz were found regarding the stomatal sensitivity to low leaf water potentials or to the root signal. Differences in the physiological and anatomical response to water deficiency as well as in the size and quality of the yield were also noted.

While measuring the diurnal changes in the physiology of grapevine leaves, Hunter *et al.* (1994) found that the highest rate of photosynthetic activity of the basal leaves occurred at or before 13:00 in the period between véraison and ripeness. The rates of activity then decreased to a minimum later in the afternoon whereafter it stabilized or even increased a little at 18:00. They ascribed the decrease in the afternoon to particularly the decrease in ambient light intensity.

During the same phenological stages Archer & Strauss (1989) found the stomatal resistance to decrease during the morning to reach a minimum at 14:00. After that it increased again to values at 18:00 that were similar to those measured in the early morning at 06:00. The graph from Smart (1974) showed a similar pattern. In contrast, according to Bravdo & Naor (1995), the stomatal resistance increased during the morning to reach a maximum at midday, whereafter it decreased again. These contradictory results could possibly have been the result of using canopies with different densities, shoots that differed in their degree of development, and measurements that were taken on vines grown under different water deficit levels.

As already discussed, the stomatal conductance is strongly affected by the soil water content (Naor & Bravdo, 1996), while both these two parameters are significantly correlated with stem water potential (Davies & Zhang, 1991; Bravdo & Naor, 1995; Naor & Bravdo, 1996; Naor, 1998) and predawn leaf water potential (Archer & Strauss, 1989). Predawn water potential values of –0.4 MPa to -0.5 MPa is indicative of water stress conditions (Lopes, 1999), which can easily be used to identify water stressed vines (Archer & Strauss, 1989). Although the predawn water potential parameter was found to be a sensitive indicator of the physiological activity of sun leaves under water stress conditions, the leaf water potential during the day was a poor indicator of sun leaf photosynthetic activity (Lopes, 1999). According to the same source the stomatal conductance was correlated with the leaf water potential, although to a lesser extent than with the stem water potential, probably because the leaf water potential is directly affected by the immediate surroundings of the canopy (Naor & Bravdo, 1996).

According to Smart (1974) the leaf water potential decreased rapidly in the early morning, due to the opening of stomata in response to the increased light intensity. It continued to decrease until around midday, whereafter it began to increase again in the late afternoon. Archer & Strauss (1989) found the leaf water potential to be most negative between 12:00 and 14:00, while Naor & Bravdo (1996) also reported a decrease in the leaf water potential during the day, whether the vines were irrigated or not.

Considering the above-mentioned patterns and correlations, diurnal patterns of certain physiological parameters measured from normally and underdeveloped shoots in shaded and well-exposed canopies were compared in an attempt to quantify any differences that may exist in the functioning of their leaves.

3. MATERIALS AND METHODS

Experimental vineyard

A seven year old *Vitis vinifera* L. cv. Shiraz, clone SH1A, grafted onto Richter 99 (*Vitis Berlandieri* x *Vitis rupestris*), clone RY2A, vineyard was used for this study. The vineyard is situated at the experimental farm of the Agricultural Research Council (ARC) Infruitec-Nietvoorbij near Stellenbosch in the Western Cape (Mediterranean climate). The vines are spaced 2.75 m × 1.5 m on a Glenrosa soil with a western aspect (26° slope) and trained onto a 7-wire lengthened Perold trellising system with movable canopy wires (VSP). Rows were orientated in a North-South direction.

Micro sprinkler irrigation was applied at pea size berry and at véraison. Pest and disease control was applied during the growth season according to the standard program of the ARC.

Experiment design

The experiment was laid out as a completely randomised 2×2 factorial design. The two factors were: degree of canopy exposure (well-exposed and shaded canopies), and level of shoot development (normally and underdeveloped shoots). There were three replications for each of the 4 treatment combinations.

Shaded canopies were only shoot positioned and topped, whereas additional suckering and leaf thinning were applied in order to create well-exposed canopies. Selection of underdeveloped shoots was based on length and comparative lack of lignification at véraison. Measurements were taken in the fifth week after véraison on 20 February 2002.

Measurements

Photosynthesis and transpiration measurements: [Also described in Hunter & Visser (1988)]. Rate of photosynthesis (mg $CO_2.dm^{-2}.h^{-1}$), stomatal resistance ($s.cm^{-1}$), rate of transpiration ($\mu g\ H_2O.cm^{-2}.s^{-1}$), photosynthetic photon flux density ($W.m^{-2}$), percentage relative humidity, internal CO_2 (μbar) and leaf temperature (°C) were measured in the vineyard with an ADC portable photosynthesis meter (The Analytical Development Co., England). The apparatus consists of an infrared CO_2 analyser, a data logger, a Parkinson broad leaf chamber and air supply unit. Volume of the chamber is 16 cm^3 and the area 6.25 cm^2. The length

of the air supply tube is 4 m. Radiation was measured using a quantum sensor with filters providing response from 400 nm to 700 nm. The maximum vapour pressure (E_{max}) was taken as two, while the airflow rate through the open system was adjusted to 300 $cm^3.min^{-1}$.

When determining daily photosynthetic cycles, measurements were taken at 08:00, 10:00, 12:00, 14:00 and 16:00 on 20 February 2002 (three replications). Sun leaves in the basal (first three leaves above the bunches) position on the shoot were measured in all the cases whereafter the measurements obtained were converted to molar units per square metre per second, i.e. rate of photosynthesis ($\mu mol.m^{-2}.s^{-1}$), stomatal conductance ($mmol.m^{-2}.s^{-1}$), rate of transpiration ($mmol.m^{-2}.s^{-1}$), photosynthetic photon flux density ($\mu mol.m^{-2}.s^{-1}$), percentage relative humidity, internal CO_2 (μbar) and leaf temperature (°C). The water use efficiency ratio (WUE) was calculated by dividing the rate of photosynthesis by the transpiration rate.

Stem and leaf water potential measurements: Diurnal leaf and stem water potential were measured on 20 February in 2002. Measurements were done by means of a pressure chamber (Scholander *et al.*, 1965) from 06:00 to 18:00 with two-hour intervals. Leaf water potential was determined by measuring the water potential of mature, apical leaves situated on the outer canopy. The leaves were placed in plastic bags just prior to excision to avoid post-excision water loss. Stem water potential was measured on leaves in the cluster region of the shoot. The leaves were enclosed in plastic bags covered with aluminium foil for at least 90 min before measurements took place. This was done to allow leaf water potential to equilibrate with the water potential of the xylem.

Statistical analyses

Due to the nature of the data, a non-parametric bootstrap analysis was used when it proved to be more practical than factorial ANOVA. The significance of the results was evaluated using 95% confidence intervals. Since only three replications were used per treatment, tendencies, rather than absolute statistical significances, were discussed. During interpretation of the figures, differences were considered significant when no overlapping of the 95% confidence intervals occurred.

4. RESULTS

Daily cycles of photosynthetic parameters and vine water potential

PPFD: The effect of canopy management practices on sunlight penetration could clearly be seen (Figs. 1 & 2). The basal leaves in the exposed canopies received significantly more PPFD through the day than those in the shaded canopies, especially at 12:00. At this time, normally developed shoots in the shaded canopies were significantly better exposed to sunlight than underdeveloped shoots, whereas no such difference was found in the well-exposed canopies. Thus it seemed as if sunlight penetration was more uniform in the exposed canopies, compared to the rather diffuse distribution of sunlight in the shaded canopies. In both the shaded and exposed canopies the highest sunlight levels received by the underdeveloped shoots were measured at 10:00, while the maximum levels for the normal shoots were measured at 12:00 (Fig. 2). This was most probably due to the angle of sunlight penetration in the morning, reaching the shorter shoots in the basal part of the canopy.

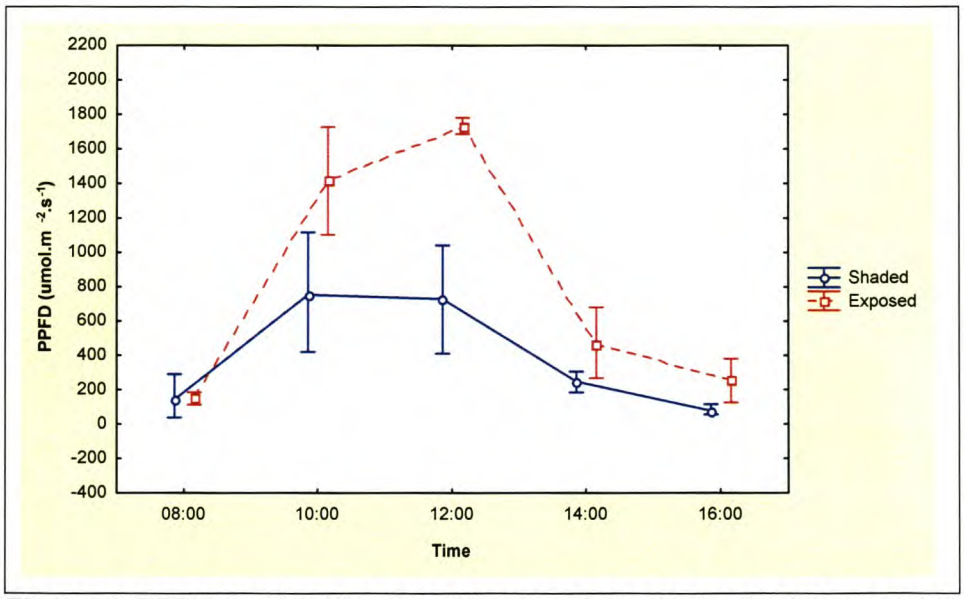

Figure 1 PPFD received by basal leaves of shoots in shaded and well-exposed canopies during the day. Error bars indicate 95% confidence intervals (bootstrap analysis).

On average, it was found that the PPFD increased from 08:00, peaked at 12:00 and decreased again to a value at 16:00 that was similar to the 08:00 measurement.

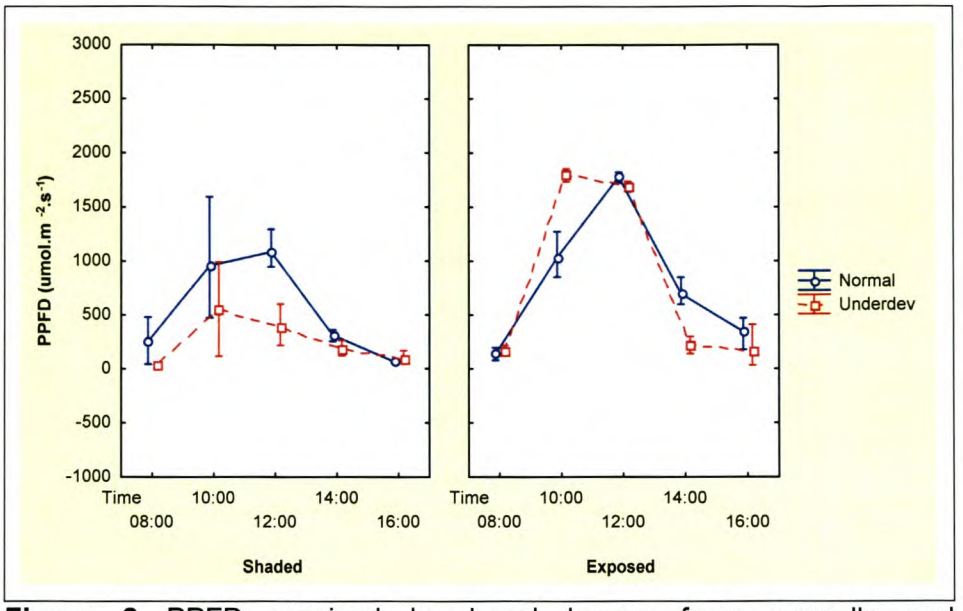

Figure 2 PPFD received by basal leaves from normally and underdeveloped shoots in shaded and well-exposed canopies during the day. Error bars indicate 95% confidence intervals (bootstrap analysis).

Leaf temperature: The temperature of all the leaves increased during the morning to reach a maximum at 12:00 (Fig. 3). Then it decreased until 14:00 where it remained constant for at least two hours.

In the shaded canopies the only difference between normally and underdeveloped shoots was measured at 12:00, where the temperature of the normal shoots was significantly higher than that of the underdeveloped shoots. In contrast, the temperature of the underdeveloped shoots was higher than that of the normal shoots in the exposed canopies, at 10:00 as well as at 12:00. The leaves on the normal shoots in the exposed canopies were cooler at 12:00 compared to those in the shaded canopies, while the leaves on the underdeveloped shoots seemed to be warmer in the exposed canopies. This is very interesting and may be ascribed to more efficient cooling of leaves on normal shoots.

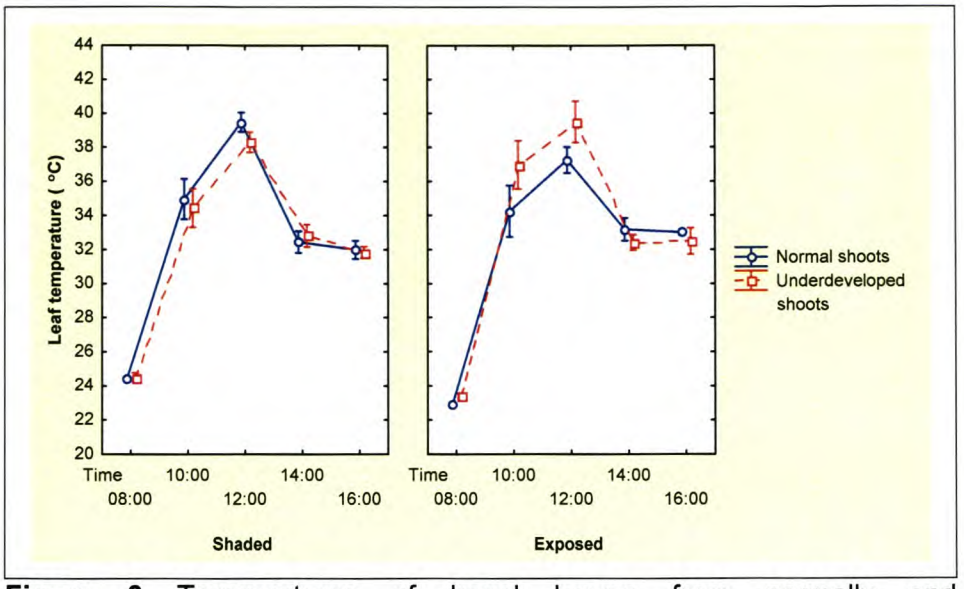

Figure 3 Temperatures of basal leaves from normally and underdeveloped shoots in shaded and well-exposed canopies during the day. Error bars indicate 95% confidence intervals.

Stomatal conductance: Except at 12:00, no significant differences were found between the stomatal conductance of leaves in shaded versus well-exposed canopies (Fig. 4). In the shaded canopies the conductance measured decreased sharply and significantly from a maximum at 10:00 to a minimum at 12:00. In the exposed canopies no significant differences were found between the values obtained at 10:00 and 12:00.

Stomatal conductance of leaves on the normally and underdeveloped shoots in the shaded canopies was similar throughout the day (Fig. 5). Both these shoot types displayed similar stomatal conductance patterns to those that occurred in shaded canopies (Fig. 4). In the exposed canopies, however, differences between the shoots were more apparent, as constantly higher levels of stomatal conductance were measured for the normally developed shoots. While the stomatal conductance of the leaves on normal shoots increased to a maximum at 10:00 and 12:00 with a subsequent decrease, the average stomatal conductivity of those on underdeveloped shoots remained more or less constant for the first part of the day. Higher levels of variation also occurred on underdeveloped shoots.

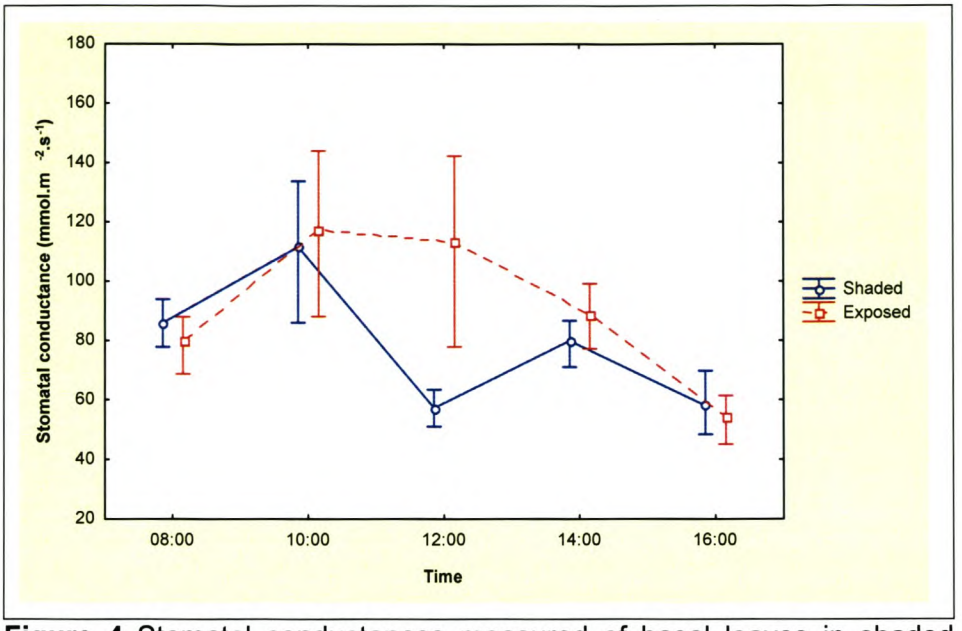

Figure 4 Stomatal conductances measured of basal leaves in shaded and well-exposed canopies. Error bars indicate 95% confidence intervals (bootstrap analysis).

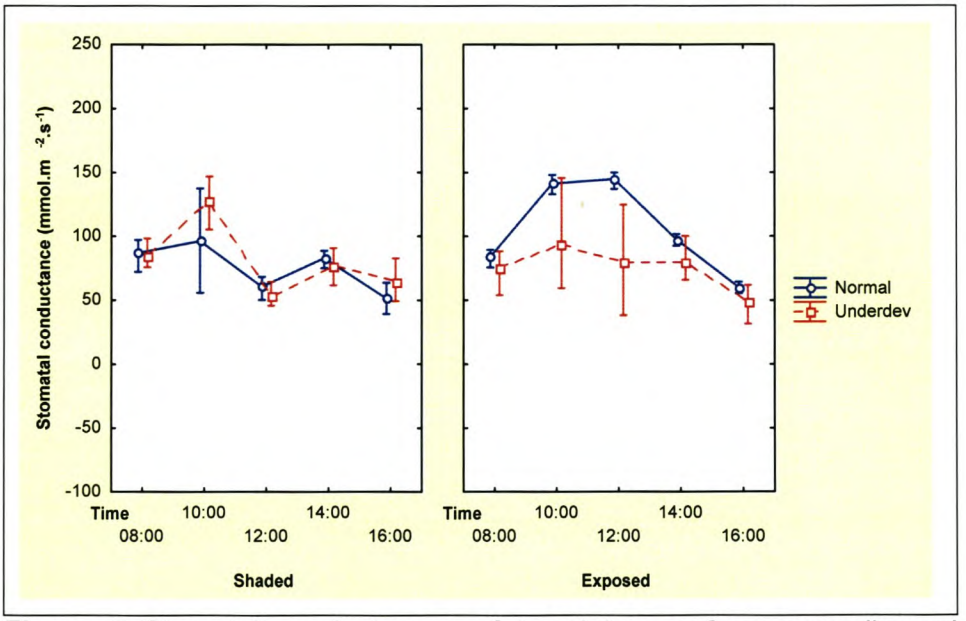

Figure 5 Stomatal conductances of basal leaves from normally and underdeveloped shoots in shaded and well-exposed canopies. Error bars indicate 95% confidence intervals (bootstrap analysis).

Transpiration rate: The degree of canopy exposure seemed to have a significant effect on the transpiration rate of the leaves at 12:00. Leaves in the exposed canopies transpired at their highest rate at this time of the day, while the transpiration rate of the leaves in the shaded canopies peaked at 10:00, followed by a gradual decline to 16:00 (Fig. 6).

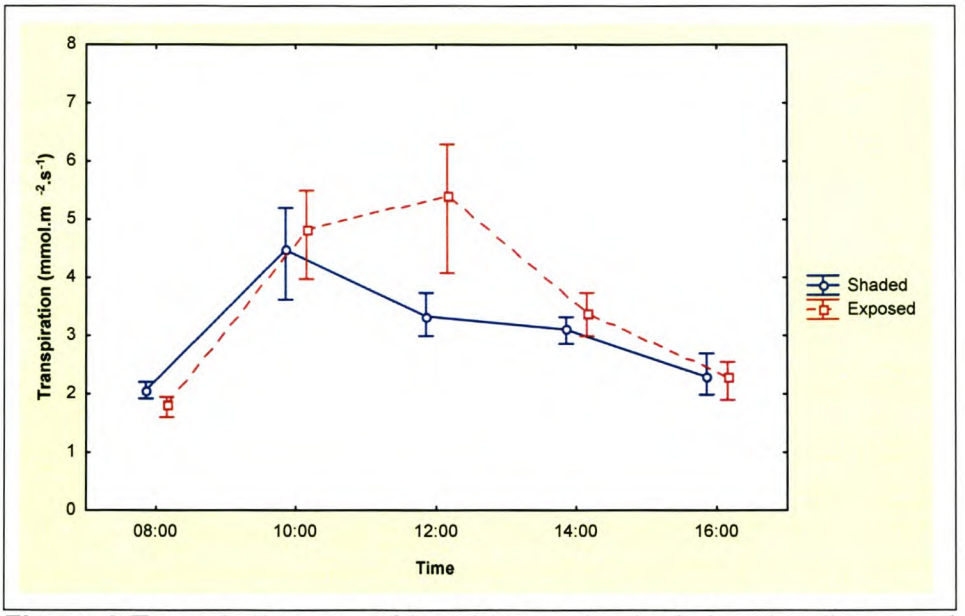

Figure 6 Transpiration rate of basal leaves in shaded and well-exposed canopies during the day. Error bars indicate 95% confidence intervals (bootstrap analysis).

No significant differences were found between the transpiration rates of leaves from normally and underdeveloped shoots during the day in the shaded canopies, while the average transpiration rate of the normal shoots seemed to be constantly higher than that of the underdeveloped shoots from 10:00 onwards in the well-exposed canopies (Fig. 7). This may explain the differences in leaf temperature between normally and underdeveloped shoots (Fig. 3). Also, the transpiration rates measured from the underdeveloped shoots displayed higher levels of variation in the exposed canopies compared to those of the normally developed shoots.

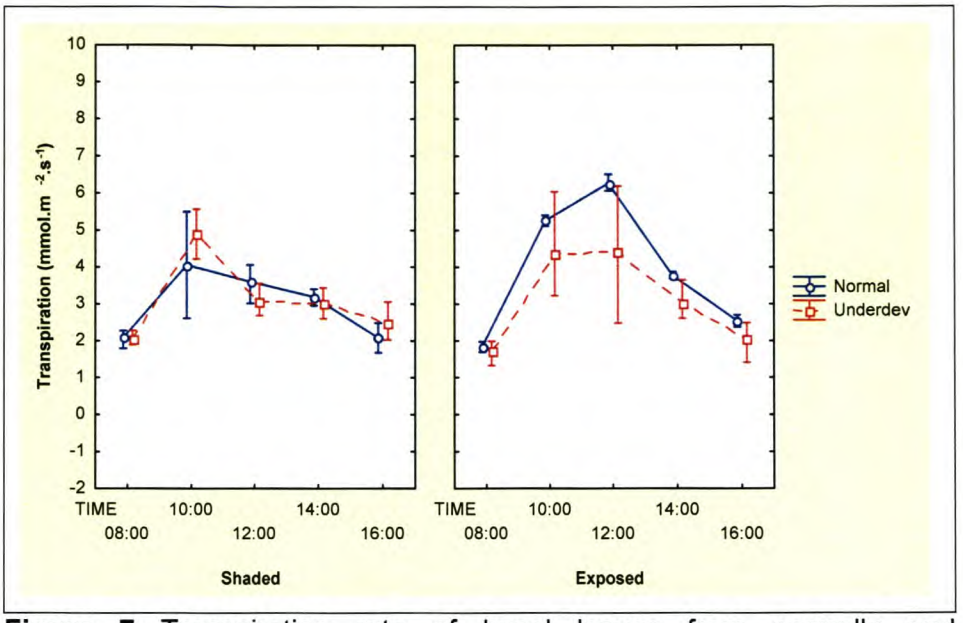

Figure 7 Transpiration rate of basal leaves from normally and underdeveloped shoots in shaded and well-exposed canopies during the day. Error bars indicate 95% confidence intervals (bootstrap analysis).

Leaf and stem water potential: Leaf and stem water potential followed typical diurnal patterns with minimum values occurring over the mid day period.

When the average leaf and stem water potentials of normally and underdeveloped shoots as well as shoots in shaded and well-exposed canopies were compared, it was clear that the leaf water potential measurements were constantly lower (Fig. 8 & 9). No significant difference in the stem water potential could be found between shaded and exposed canopies (Fig. 8), while the leaf water potential measurements were more erratic with rather large differences at 12:00 and 18:00. The leaves in shaded canopies seemed more protected against changing environmental conditions compared to those in exposed canopies.

There was also no statistically significant difference found for the stem water potential of the normally and underdeveloped shoots during the day (Fig. 9). Although the leaf water potential measurements followed a more irregular pattern with the most pronounced difference at 14:00, no significant difference in leaf water potential was found.

The leaf water potential of the normally developed shoots did not differ significantly from that of the underdeveloped shoots in the shaded or well-

exposed canopies (Fig. 10). The same seemed to be the case for stem water potential (data not shown).

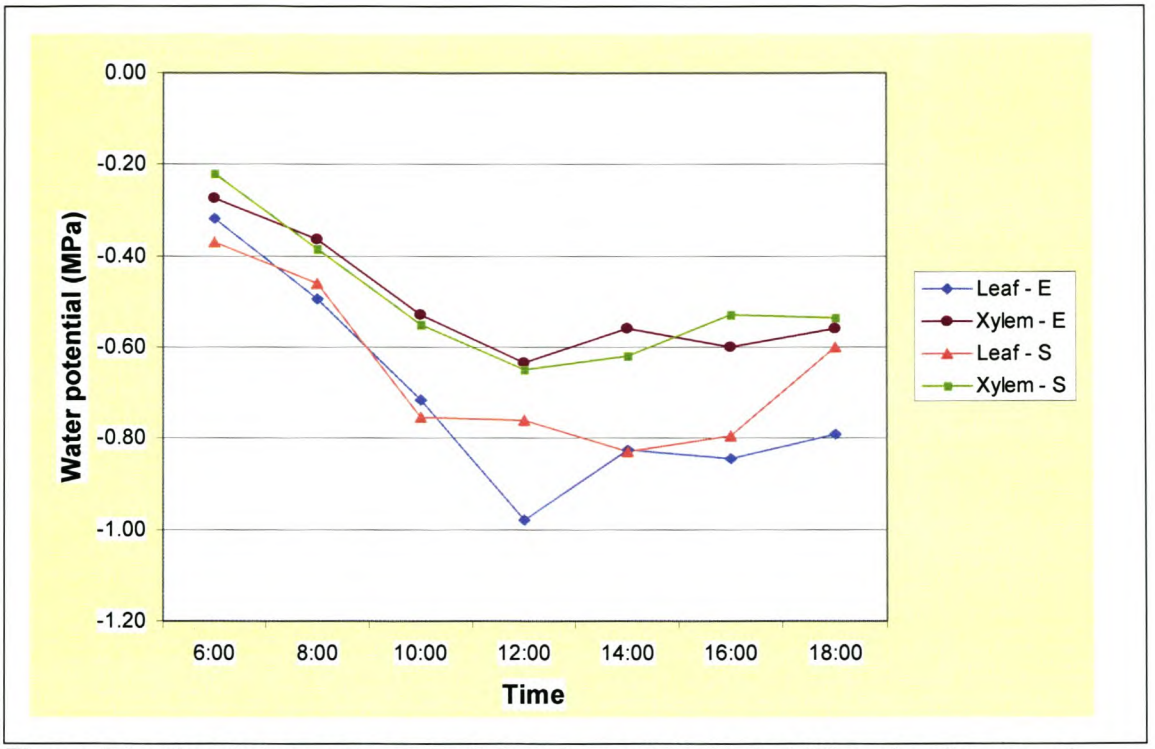

Figure 8 Leaf and stem water potentials measured in shaded (S) and well-exposed (E) canopies.

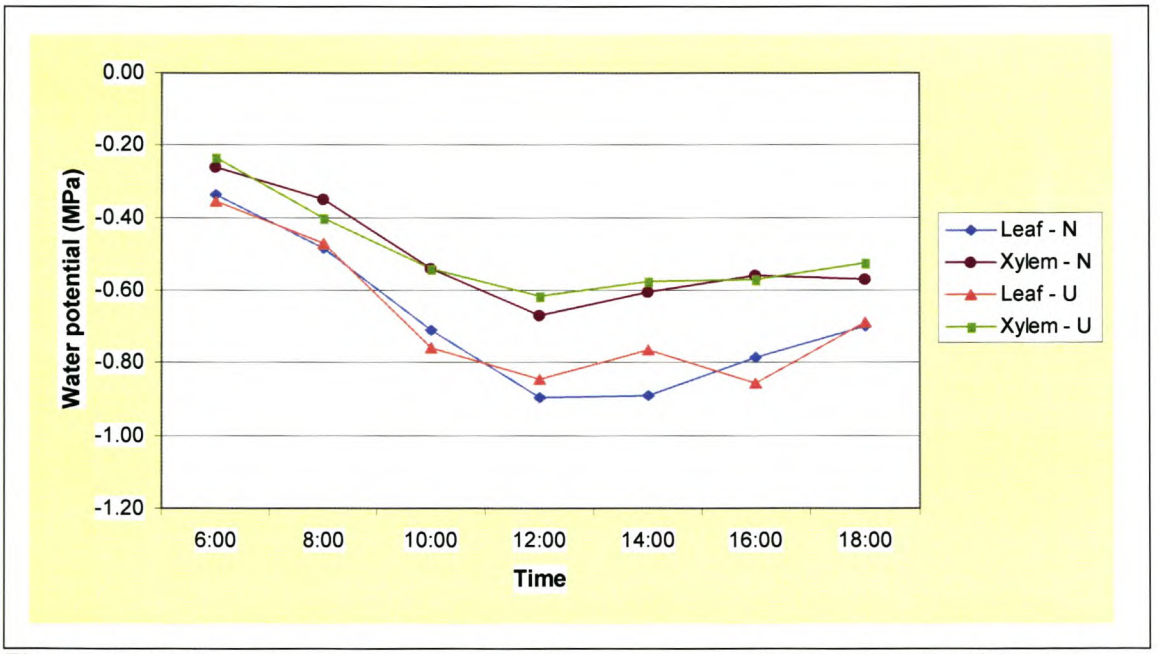

Figure 9 Leaf and stem water potentials measured from normally (N) and underdeveloped (U) shoots.

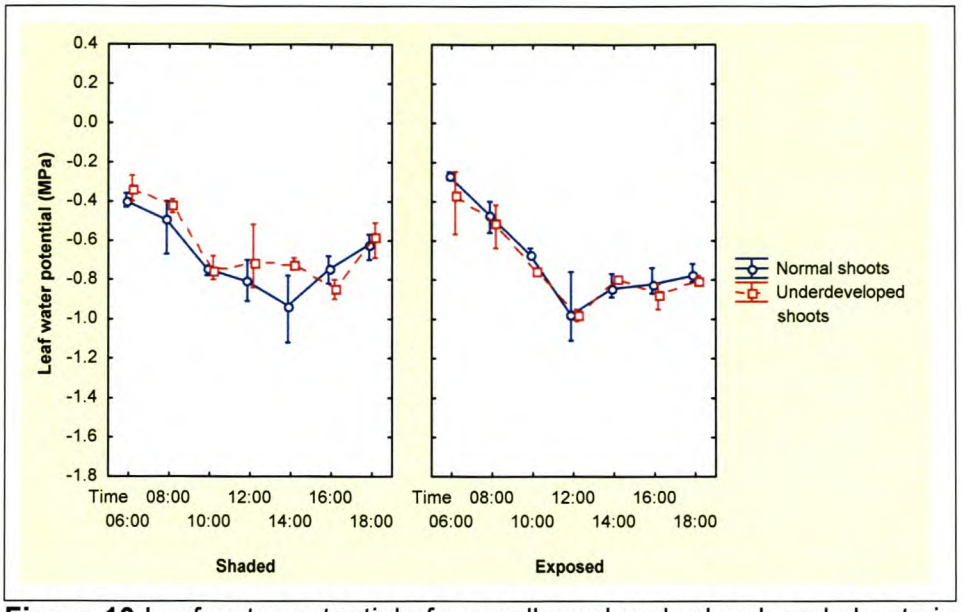

Figure 10 Leaf water potential of normally and underdeveloped shoots in shaded and well-exposed canopies during the day. Error bars indicate 95% confidence intervals (bootstrap analysis).

Photosynthetic rate: Although not statistically significant, all the shoots in the exposed canopies displayed higher rates of photosynthesis than those in the shaded canopies, especially at 10:00 and 12:00 (Figs. 11 & 13). Leaves from normally developed shoots photosynthesised at higher rates than those from underdeveloped shoots, with statistically significant differences at 12:00 and 14:00 (Fig. 12). In the late afternoon (16:00), photosynthetic activity of both shoot types was similar in shaded and well-exposed canopies (Fig. 13).

The maximum photosynthetic activity for the normal shoots in the exposed canopies was measured at 12:00, compared to the earlier maximum measured at 10:00 in the shaded canopies. Regarding the activity of the leaves on the underdeveloped shoots, it seemed as if it peaked earlier in the exposed canopies at 10:00. The measurements in the shaded canopies showed a high degree of variance at 10:00. The photosynthetic activity of leaves on underdeveloped shoots in shaded canopies remained relatively constant between 08:00 and 14:00, before it decreased to a minimum at 16:00 (Fig. 13).

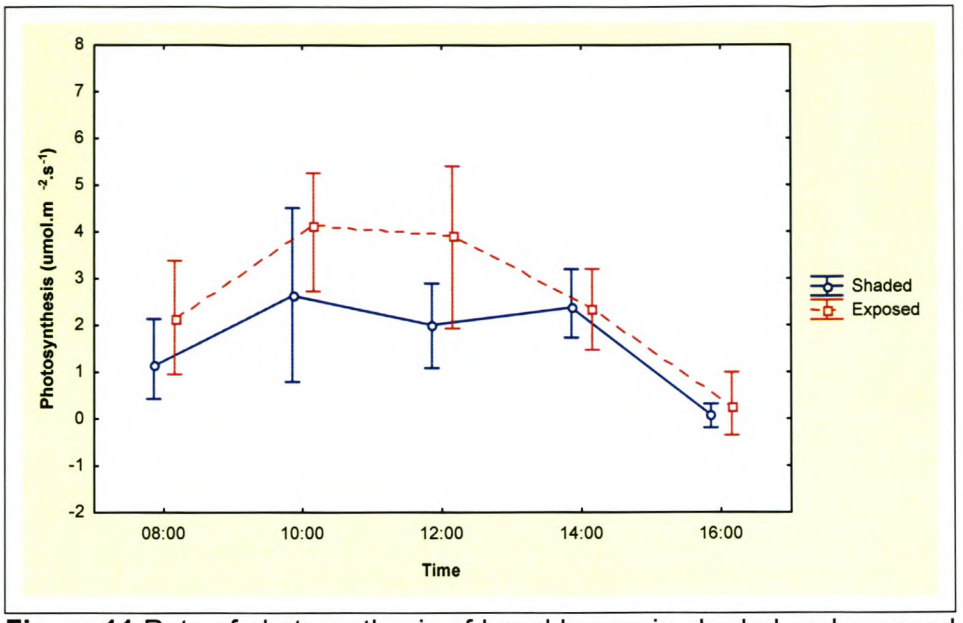

Figure 11 Rate of photosynthesis of basal leaves in shaded and exposed canopies during the day. Error bars indicate 95% confidence intervals (bootstrap analysis).

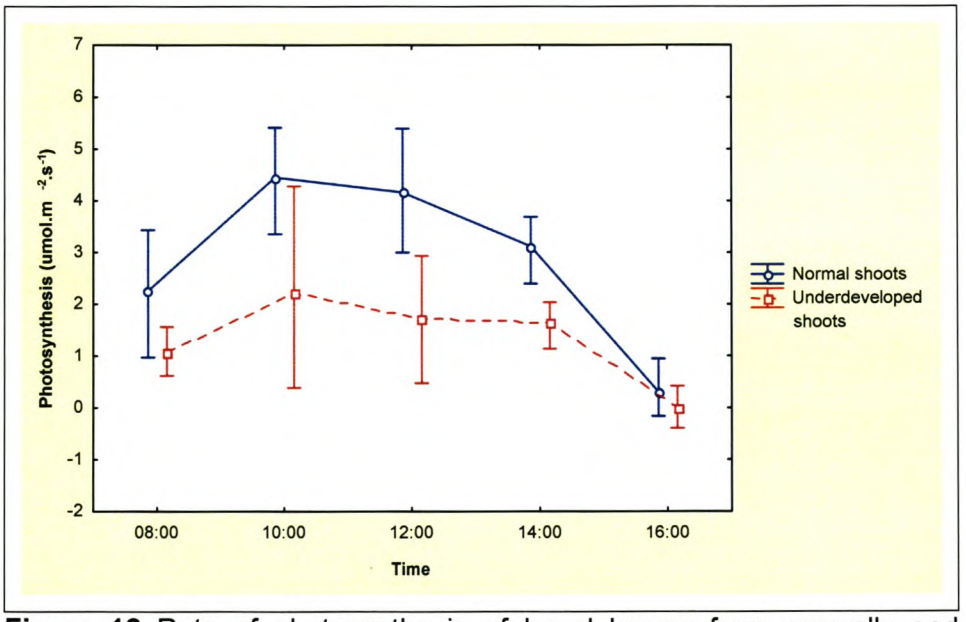

Figure 12 Rate of photosynthesis of basal leaves from normally and underdeveloped shoots during the day. Error bars indicate 95% confidence intervals (bootstrap analysis).

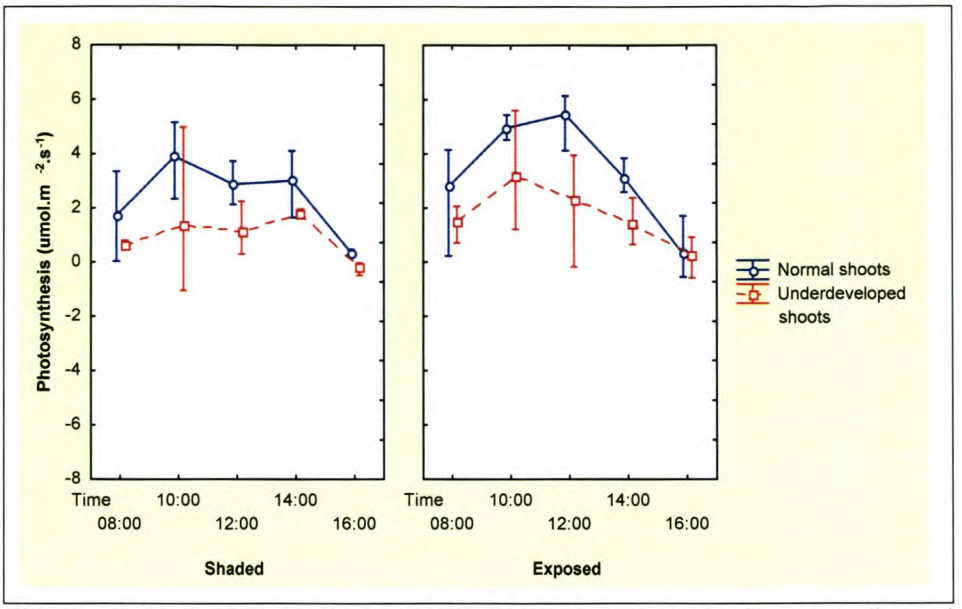

Figure 13 Daily cycles of photosynthetic rate measured for normally and underdeveloped shoots in shaded and well-exposed canopies. Error bars indicate 95% confidence intervals (bootstrap analysis).

Internal CO_2: No significant difference in the internal CO_2 levels of leaves in the shaded and exposed canopies was found (Fig. 14). Leaves on underdeveloped shoots displayed higher internal CO_2 levels than those on normally developed shoots. It seemed as if the difference between normally and underdeveloped shoots were more pronounced in shaded than in exposed canopies, with the largest difference being earlier in the day (between 10:00 and 12:00 compared to 14:00).

WUE: All the leaves on the normally and underdeveloped shoots and under shaded as well as well-exposed conditions displayed similar patterns of WUE during the day. The ratio tended to stay relative constant between 08:00 and 14:00, whereafter it decreased to a minimum at 16:00 (Figs. 15 & 16).

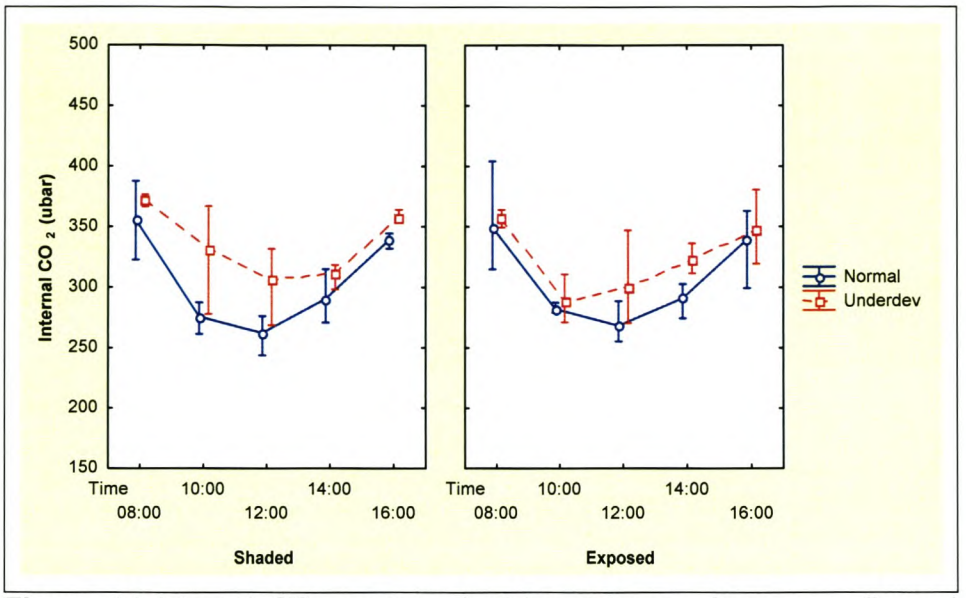

Figure 14 Internal CO_2 measured of basal leaves from normally and underdeveloped shoots in shaded and well-exposed canopies. Error bars indicate 95% confidence intervals (bootstrap analysis).

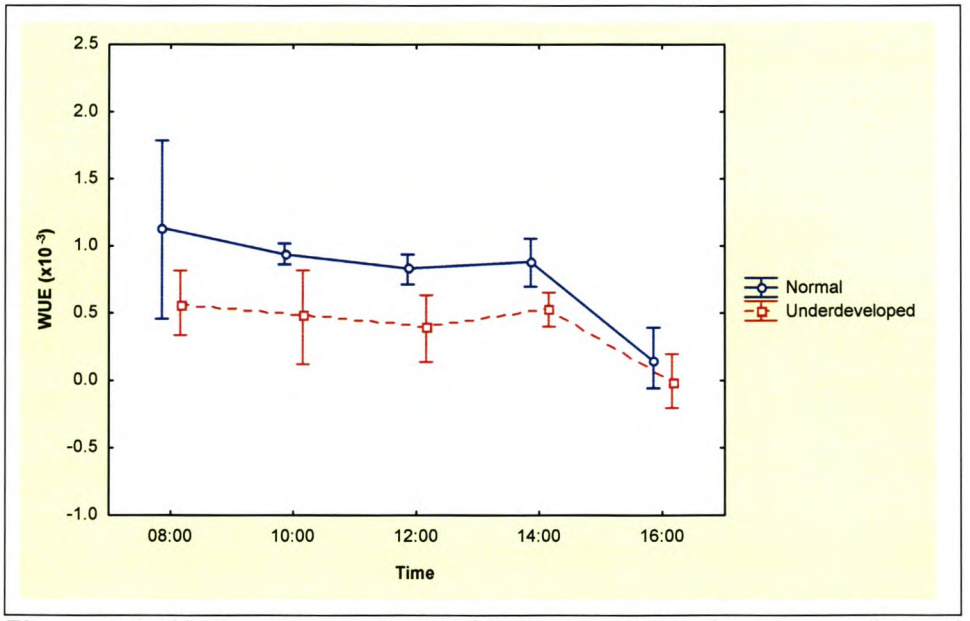

Figure 15 WUE ratio calculated for basal leaves from normally and underdeveloped shoots during the day. Error bars indicate 95% confidence intervals (bootstrap analysis).

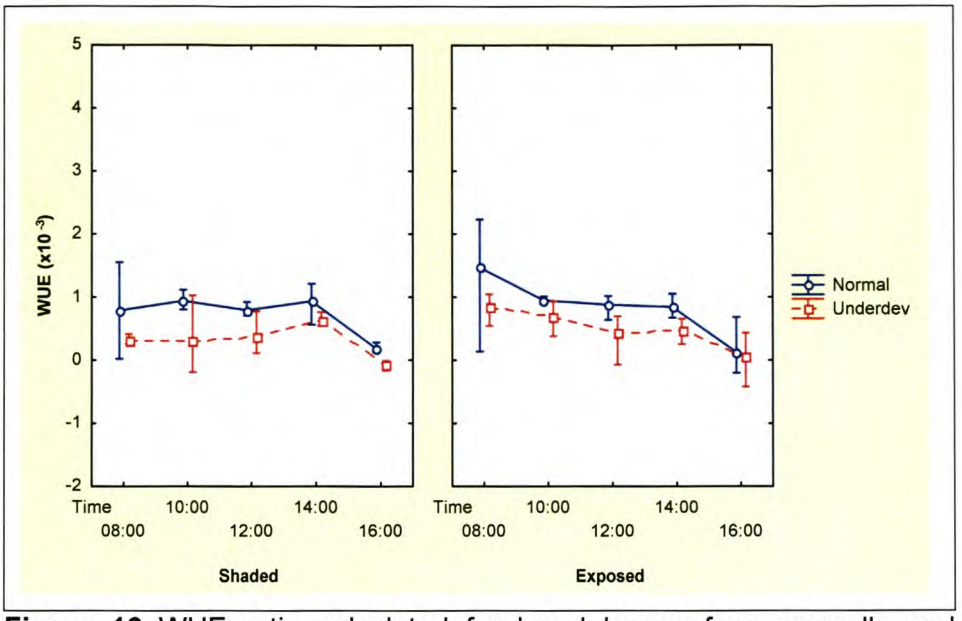

Figure 16 WUE ratio calculated for basal leaves from normally and underdeveloped shoots in shaded and well-exposed canopies during the day. Error bars indicate 95% confidence intervals (bootstrap analysis).

The leaves on normally developed shoots displayed higher ratios of WUE than those on underdeveloped shoots from 08:00 to 14:00, with significant differences at 10:00 and 14:00. No difference between the shoots was found at 16:00 (Fig. 15). When the degree of canopy exposure was also taken into account, the difference between the shoot types was not pronounced, although a higher ratio still occurred for the normal shoots (Fig. 16).

5. DISCUSSION

The diurnal pattern of stomatal conductance in the exposed canopies is in accordance with the measurements of Smart (1974) and Archer & Strauss (1989). The conductance was found to be the highest between 10:00 and 12:00 in these canopies, depending on the level of shoot development, whereafter it decreased during the afternoon.

In the exposed canopies the stomatal conductance of the normal shoots was higher than that of the underdeveloped shoots at 10:00 and 12:00, before it decreased to levels similar to that of the underdeveloped shoots at 16:00. The values found at 10:00 and 12:00 are complimented by the high transpiration rates (Fig. 7), which explain the lower leaf temperatures found for normal compared to underdeveloped shoots in the exposed canopies (Fig. 3). The higher degree of

water loss from the normal compared to the underdeveloped shoots in the exposed canopies had no effect on the leaf water potential. At 12:00 no significant difference in the leaf water potential was found between the shoot types, although a much higher degree of variance was noticed for the normal shoots.

In the shaded canopies, however, this picture was quite different. Although a peak was measured at 10:00, the stomatal conductance decreased to a minimum at 12:00, whereafter it seemed to stabilize or even recover during the afternoon. Bravdo & Naor (1995) also found the stomatal conductance to reach a minimum at midday before it increases again in the afternoon, but the shape of the curve was not similar to that of the shoots in the shaded canopies (Fig. 5).

The low level of stomatal conductance of underdeveloped shoots in shaded canopies at 12:00 could be due to the rather low PPFD measured at the same time (Fig. 2). However, since the light intensity remained at that same low level during the afternoon while the conductance seemed to increase somewhat, it seemed that other factors than the PPFD also affected the stomatal conductance. This is supported by the fact that although the normal shoots in the shaded canopies received significantly higher levels of PPFD than the underdeveloped shoots, their stomatal conductance still decreased to a minimum at 12:00 that did not differ significantly from that of the underdeveloped shoots.

The high leaf temperature of almost 40°C measured at 12:00 in the shaded canopies could have played a role in the closure of the stomata. According to Kriedemann (1977) the vine leaves suffer more from tissue desiccation than from high temperatures as such. He found that when the leaves were kept hydrated, temperatures up to 49°C were endured without any obvious damage to the leaves. Therefore, closure of the stomata probably occurred in order to prevent excessive water loss that would result in tissue desiccation.

If this proved to be true, it could be assumed that the rate of transpiration would have decreased at 12:00 while the leaf water potential will remain constant or even increase due to the stomatal closure. Although the stomatal conductance of both the normally and underdeveloped shoots decreased at 12:00 in the shaded canopies (Fig. 5), only the transpiration rate of the underdeveloped shoots decreased significantly between 10:00 and 12:00 (Fig. 7). The higher light intensity and leaf temperature of the normal shoots at 12:00 could explain this, since water loss through the leaf can still occur under high temperatures

despite the closed stomata (Schultz, 1997). The result is a decrease in leaf water potential of the normal compared to the underdeveloped shoots in the shaded canopies at 12:00 and 14:00 (Fig. 10).

The leaf water potential measurements through the day are in accordance with the patterns described by Smart (1974), Archer & Strauss (1989) and Naor & Bravdo (1996). According to Smart (1974) leaf water potential measurements of –1.3 MPa is low enough to induce stomatal closure. Kriedemann (1977) did not mention a specific value, but stated that if the transpiration rate exceeded the rate of water supply to the leaf, the moisture stress that will develop inside the leaf would induce closure of the stomata. At no time during the day did the water potential of the leaves from the normal or underdeveloped shoots in the shaded or exposed canopies exceed the threshold value of –1.3 MPa. It therefore never seemed as if any of the leaves functioned under water stress conditions. According to Lopes (1999) predawn leaf water potential measurements of around –0.4 MPa to –0.5 indicated water stress conditions in the soil. From the data in Fig. 10, it seemed as if there could be a small degree of water deficit in the soil and it was assumed that, despite the rather high leaf water potential measurements during the day, a root signal was probably produced and transported to the leaves to act as an early warning system regarding soil water content.

The results of Schultz (1996; 1997) indicated that stomatal conductance in a Shiraz leaf will continue at low water potential, since the stomata are dependent on the root signal for closure. So even under water stress conditions the leaves will continue to transpire in the absence of a root signal. As already stated, despite rather similar water potential patterns for the normal and underdeveloped shoots in the shaded and exposed canopies, big differences in the diurnal stomatal conductance patterns were noticed between the canopies as well as between the shoots in a specific canopy.

The available soil water content was considered to be the same for all the vines involved, since the treatments were carried out in one block with a relatively homogeneous soil, all the vines were grafted onto the same rootstock cultivar, and no significant differences were found between the predawn water potential measurements for the different shoot types and/or the different degrees of canopy exposure. Also, the water status of all the vines was considered the same, since no significant difference was found in the stem water potential between the different shoots or the differently exposed canopies during the day

(Figs. 8 & 9). If a root signal was produced and transported in all the vines, and it was assumed that it was relatively uniform in concentration, it seemed as if the shoots in the well-exposed and shaded canopies reacted differently to it. The same applied for the respective shoot types in a particular canopy.

According to Düring *et al.* (1996), when the ABA concentration in the roots and thus transpiration stream increases, closure of stomata will be induced. Apparently, Tardieu & Davies (1993) found that leaves differ in their sensitivity to the signal, depending on their water potential (Düring *et al.,* 1996). Another possible reason for differential stomatal closure within a canopy could be an uneven distribution of the ABA-root signal within a canopy. Stomatal closure will most likely occur first in leaves that receive the highest ABA concentration from the transpiration stream, or those that are the most sensitive to it. Unfortunately, since no direct assessment of the ABA concentration in the vine was made, some of the statements in the following paragraph are speculative.

Despite the lower stomatal conductance and transpiration rate of the underdeveloped shoots in the exposed canopies, no significant difference in leaf water potential between the normally and underdeveloped shoots was found at midday (Fig. 10) and therefore a difference in sensitivity to a possible root signal due to low water potentials may possibly be ruled out. Factors other than a root signal most probably also played a role. It thus seemed as if the normally developed shoots were kept better hydrated by the vine than the underdeveloped shoots.

It appeared as if water distribution inside the vine is similar to the way photosynthetic assimilates are distributed, namely according to the sink strength, i.e. according to changes in water potential gradients. The more physiologically active shoots with higher transpiration rates most probably imported water (and minerals) at a faster rate to maintain leaf turgor and support physiological activity. Although most of the potassium in grapevines is transported by the phloem sap (Ollat & Gaudillère, 1995), a small amount of potassium is also transported by the xylem. When potassium is pumped into the guard cells of the stomata, the water potential in these cells decreases and water moves in due to the concentration gradient. Turgidity of the guard cells will increase and opening of the stomata will occur (Archer, 1981, and references therein). This could be a possible mechanism how leaves on normal shoots are kept hydrated while continuing with physiological activity (transpiration and photosynthesis) under limited water conditions.

In both the shaded and the well-exposed canopies the normal shoots displayed higher rates of photosynthesis than the underdeveloped shoots, while the maximum photosynthetic rate of the normal shoots in the exposed canopies exceeded that of the normal shoots in the shaded canopies at 12:00.

The levels of PPFD could have affected the diurnal pattern of photosynthesis, since, in shaded canopies, normal shoots received higher light intensities than underdeveloped shoots at 10:00 and 12:00. However, similar PPFD values were measured for the shoots at 14:00, which do not explain the higher photosynthetic activity of the normal shoots. Although light could have played a role at 14:00 in the exposed canopies, other factors were more important during the morning and at midday, since either no difference in the light intensity received by the different shoots was measured, or a higher PPFD was measured for the underdeveloped shoots. The angle of radiation in respect to the canopy and/or the position of the different shoot types within the canopy may have played a role in this regard.

In accordance with the findings of Hunter *et al.* (1994) the photosynthetic activities of all the shoots were relatively high at 08:00, considering the sub-optimal light conditions. The same applies to the measurements taken at 14:00. According to Champagnol (1984) the optimal light intensities for photosynthetic activity is between 704 $\mu E.m^{-2}.s^{-1}$ and 1100 $\mu E.m^{-2}.s^{-1}$.

Consistent with Smart (1987), a relationship existed between the PPFD and the leaf temperature, since both increased during the morning and peaked at 12:00, followed by a decline in the afternoon. The optimum temperature for photosynthesis is considered to be 25°C (Kriedemann, 1977; Alleweldt *et al.*, 1982), while variation in temperature between 16°C and 29°C did not affect the rate of photosynthesis under field conditions (Archer, 1981). Extremely high temperatures also affect photosynthesis negatively due to leaf tissue desiccation (Kriedemann, 1977). Leaf temperatures were found to be as high as 37-39°C at 12:00 (Fig. 3), which are according to literature too high for optimum photosynthetic activity. The highest rates of photosynthesis during the day were, however, measured between 10:00 and 12:00 and it was assumed that the leaves were sufficiently hydrated during that time to continue to photosynthesise unimpeded (Fig. 10).

Observed instantaneous rates of photosynthesis are dictated by environmental conditions such as water supply, light, temperature, CO_2, and O_2 as well as

internal control mechanisms that affect overall demand for photosynthetates and partitioning of assimilates within the vine (Huglin, 1972, according to Kriedemann, 1977). The leaf area in relation to crop load is amongst the factors mentioned by Petrie *et al.* (2000) that could affect the photosynthetic rate of individual leaves. The significantly lower ratio of total leaf area per gram fresh berry mass found for underdeveloped compared to normal shoots (Chapter 6) could have resulted in an increase in the photosynthetic rate (Kriedemann, 1977; Hunter, 1991). However, photosynthesis can only be increased up to a certain point as dictated by internal physiological mechanisms and restrictions and by environmental, especially microclimatic, conditions. The possibility of physical restriction of photosynthesis in leaves on underdeveloped shoots (due to poorly differentiated palissade and mesophyll cells) was discussed in Chapter 4, as well as the sub-optimal microclimate of underdeveloped compared to normally developed shoots.

The pattern of photosynthetic activity during the day is very similar to the stomatal conductance, which is well expected since the CO_2 used during photosynthesis diffuses into the mesophyll of the leaf through the open stomata. The internal CO_2 levels of the leaves also reflect the changes in photosynthetic activity through the day, since higher levels or an increase in internal CO_2 indicates a low rate of assimilate transport from the leaf that will result in an accumulation of CO_2 within the vine leaf (Chapter 4). The decrease in photosynthetic activity during the afternoon is in accordance with the findings of Hunter *et al.* (1994) who ascribed it to a decrease in ambient light intensity.

The beneficial effect of canopy management practices on vine functioning is once again illustrated by this study of the diurnal patterns of certain physiological parameters. During the day, higher levels of sunlight penetration, stomatal conductance and transpiration, as well as photosynthetic rates were measured for especially the normally developed shoots in the well-exposed compared to the shaded canopies. This is in accordance with the findings discussed in Chapter 4.

6. CONCLUSIONS

Stomata are very important for maximal physiological activity in the vine leaf, as they control atmospheric CO_2 assimilation for photosynthesis as well as the loss of water through transpiration. Since stomatal closure will occur when the

transpiration rate exceeds that of the water supply to the vine (Kriedemann, 1977), stomatal conductance will be affected by the available water status in the soil. Predawn leaf potential measurements correspond with the available soil water content (Archer & Strauss, 1989), since it quantifies the hydric status of the vine in direct relation to the soil water that is accessible to the roots (Deloire, 2003, personal communication).

ABA root signals explain why decreased stomatal conductance often preceeds changes in leaf water potential (Düring *et al.* 1996, and references therein). Despite various statements in the literature on the stronger correlation between stem water potential and stomatal conductance, it was decided to concentrate more on the leaf water potential. Because the stem water potential is well correlated with the whole vine water status and the leaf water potential is easily affected by atmospheric conditions, the latter should be more useful in quantifying differences between various shoots of the same vine and quantifying "in-time" changes and patterns.

When the day cycles of certain physiological parameters were compared for normally and underdeveloped shoots in shaded and well-exposed canopies, it was found that the largest differences occurred between 10:00 and 14:00, while the measurements taken at 08:00 and 16:00 were quite similar in most cases. Differences therefore occurred during the period of most extreme environmental impact.

From the predawn leaf water potential values it seemed as if there could be a small degree of water deficiency in the soil, since it was very near to the threshold value of –0.4 MPa found by Lopes (1999). It was assumed that a root signal was probably produced and transported to the leaves to act as an early warning system regarding soil water content, although the rather high average leaf water potential measurements of minimum –1.0 MPa during the day could have shown that the leaves were sufficiently hydrated for physiological activity. According to Smart (1974) values of –1.6 MPa and lower can induce stomatal closure due to water deficiency inside the vine leaf. The findings of Schultz (1996), however, indicate that Shiraz leaves are not very sensitive to low leaf water potentials and can continue with photosynthesis and transpiration where stomatal closure of leaves from other cultivars would have occurred. They further concluded that Shiraz leaves are dependent on a root signal to induce stomatal closure under water stress conditions.

It seemed as if vine shoots could differ in their response to a root signal, depending on the degree of canopy exposure and/or the level of shoot development, which would lead to differences in physiological activity through the day. The normally developed shoots in the well-exposed canopies were physiologically the most active (highest rates of photosynthesis and transpiration) at 12:00 when the leaf water potential was the lowest and the highest degree of water stress in the shoots was expected. It was concluded that either the water status of the leaves was not sufficient enough to induce stomatal closure, or the leaves did not receive a strong enough root signal (or was not sensitive enough) for the stomata to close.

Another possibility mentioned was that the water transport and distribution within the vine occurred on the same principles as assimilate transport, namely according to sink strength. The more actively photosynthesising and transpiring shoots would thus have a stronger demand for water to maintain water potential and their physiological activity. Water could thus possibly be preferentially transported to those shoots compared to less active shoots, while redistribution of water from the latter shoots could also occur.

The positive effect of canopy management practices on physiological activity in the canopy was very well illustrated. In Chapter 4 it was found that leaves on shoots in well-exposed canopies received higher levels of PPFD and displayed higher rates of photosynthesis and transpiration, while lower stomatal resistance and internal CO_2 levels were measured. All these parameters were measured at 10:00 and the differences were not found to be statistically significant. While measuring the day cycles of the same parameters, higher maximum levels of PPFD, photosynthesis, transpiration and stomatal conductance were also measured in the exposed than in the shaded canopies, with significant differences in PPFD, transpiration and stomatal conductivity at 12:00.

Smart *et al.* (1985) stated that physiological functioning of the canopy affects the fruit composition and ultimate wine quality. Since canopy management practices were conducive to the functioning of the leaves, it was expected that the grape quality would also be positively affected.

Important differences in the physiological activity between normally and underdeveloped shoots also became apparent. In Chapter 4 the differences between the shoots at 10:00 and the possible factors affecting it, were discussed. Normal shoots received higher levels of PPFD, while the leaves showed lower

stomatal resistance and internal CO_2 levels. Significantly higher photosynthetic and transpiration rates were measured while a higher WUE ratio was also calculated for the normal shoots.

When the day cycles were plotted, it was found that the leaves of the normal shoots did not necessarily receive higher light intensities than those on the underdeveloped shoots (as was found in Chapter 4) – this was only noted in the shaded canopies from late morning until early afternoon. Sunlight penetration seemed to be more uniform in the exposed canopies, with all the shoots exposed to the same light intensity at 12:00. Despite the differential radiation received, higher stomatal conductance, transpiration rates and significantly higher photosynthetic rates were measured at midday for the normal compared to the underdeveloped shoots. The physiological functioning of the normal shoots were also more efficient in terms of water relations, since significantly higher WUE ratios occurred in these shoots between 10:00 and 14:00. Internal factors, such as the total leaf area per gram fresh berry mass produced, that could have affected the activity of the leaves, were discussed in Chapter 4.

It was therefore found that the physiological functioning (rates of photosynthesis and transpiration) of leaves from normal shoots was superior to those on the underdeveloped shoots. If it is further taken into account that normal shoots had significantly more total leaf area per shoot than the underdeveloped shoots, it was assumed that the total carbohydrate production by normal shoots would also have been significantly higher. Since the grape berries are the most important sinks for assimilates during the ripening period (Koblet, 1977), it is expected that the size and quality of the yield of normally developed shoots will be higher than that of underdeveloped shoots.

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CHAPTER 6

RESEARCH RESULTS

THE EFFECT OF SHOOT HETEROGENEITY ON REPRODUCTIVE GROWTH PARAMETERS OF SHIRAZ/RICHTER 99 GRAPEVINES

1. ABSTRACT

In this study the physiological potential of normally and underdeveloped shoots was compared in an attempt to quantify the effect of shoot heterogeneity in a Shiraz/Richter 99 vineyard. The field trial was performed in the Stellenbosch area, Western Cape, South Africa. Comparisons based on certain reproductive growth parameters were made between normally and underdeveloped shoots from shaded and well-exposed canopies. A higher total number and more shoots per metre cordon length were found in the shaded compared to the exposed canopies, with a lower percentage normal and higher percentage underdeveloped shoots. The percentage fertility of the normal shoots was lower in the shaded canopies, while a greater extent of shoot heterogeneity also existed. Cluster size seemed to be fixed before véraison. The degree of canopy exposure had no effect, while clusters on normal shoots were significantly larger than those on underdeveloped shoots. More berries per cluster were found for the underdeveloped shoots in the exposed canopies, while canopy management did not affect the number of berries per cluster for the normal shoots. Significantly more berries were found in the clusters of normal compared to underdeveloped shoots, which was probably due to better carbohydrate nutrition. The growth and ripening curve of the berries from underdeveloped shoots seemed delayed because of over-cropping of the shoots. Together with the larger berries and lower skin:pulp ratio found for the underdeveloped shoots, it is expected that berries from normal shoots will be better ripened with more intense flavour and colour. Canopy management practices should further improve the berry quality of the normal shoots, since it seemed as if carbohydrate accumulation during the ripening phase was impaired in the shaded canopies.

2. INTRODUCTION

Wine industries all over the world are committed to produce grape and wine quality suited to meet the challenges of ever-increasing national and international market competition and requirements (Hunter & Archer, 2001). Meeting those requirements often includes an increase in grape and wine quality without a decrease in the yield or longevity of the vine. Therefore, carbon allocation to the clusters must be optimised (Hunter, 2000) without detrimentally affecting the

growth and development of other parts of the vine. A skilful and comprehensive management strategy, which includes long and short-term cultivation practices, is hence needed (Hunter & Archer, 2001).

According to Carbonneau (1995) the yield, berry maturation and wine quality are dependent on the canopy structure, as it defines the microclimate and thus the photosynthetic activity of the canopy. Photosynthesis is particularly important in relation to the total yield and the distribution of assimilates to the different plant parts (Calò *et al.*, 1995) – thus improved radiation due to canopy management of vigorous vines will lead to an increase in yield as all yield components are affected by shade (Smart *et al.*, 1990).

The effect of budding percentage and shoot fertility on the yield is obvious. The development of fruit buds is an important factor in determining the size and profitability of the yield (Swanepoel & Archer, 1988). According to the same source (and references therein) the development of inflorescences and flowers in grapevines comprise three well-defined phases: the initiation of anlagen, the formation of inflorescence primordia and the development of flowers.

Of course the formation of fruit buds is meaningless unless the buds are able to sprout. It was found that low light intensities in the basal part of the canopy decreased the budding percentage and bud fertility (Archer, 1988; Hunter, 1991). According to Winkler *et al.* (1974), May (1965) and Sartorius (1968) found that it is the light actually falling on the bud itself that affects its fruitfulness, rather than whole plant illumination. Apart from this direct stimulating effect of light, it also has an indirect effect due to the linear relationship with temperature (Smart, 1987). Antcliff & Webster (1955) found that weather conditions directly affected the fruitfulness of the buds produced that year (Winkler *et al.*, 1974).

It can be stated that all factors and cultivation practices that improve the canopy exposure to light and induce normal vigour and physiological functioning of the shoots, will be conducive to vine bud fruitfulness. Lavee *et al.* (1967) showed that a certain amount of leaf area is needed for induction of fruit primordia in grape buds (Winkler *et al.*, 1974).

The formation of inflorescence primordia occurs in the preceding season, while the development of the flowers occurs within 10 to 15 days of appearance of the inflorescence (Swanepoel & Archer, 1988). The stage of development of the fruit bud at the time that shoot growth began, affected the rate of its continuing

development. Flower clusters of young shoots on normal, well-ripened spurs will be more advanced in development than those on weaker spurs. This difference is very seldom overcome (Winkler *et al.*, 1974).

May *et al.* (1973) stated that poor fruit set is a primary limitation to yield in the grapevine (Kriedemann, 1977). According to Winkler *et al.* (1974) two schools of thoughts exist as to what regulates fruit set in grapevines - one group maintain that specific fruit setting factors (growth regulators) regulate fruit set, while according to the other group fruit set is regulated by the supply of organic nutrients. Strong evidence has apparently been provided by Mullins (1967) that fruit set is solely regulated by the supply of organic nutrients. It may well be that both these physiological factors impact on fruit set and that the prevailing environmental conditions largely affect this process.

Keller & Hrazdina (1996) found that a low nitrogen supply during bloom reduced fruit set due to inflorescence necrosis. Caspari & Lang (1996), on the other hand, linked fruit set with the carbohydrate supply, as symptoms similar to early bunch stem necrosis (EBSN) increased as the carbohydrate supply decreased. All practices and/or factors that affect the carbohydrate availability, such as extreme temperatures, water deficiency, inadequate leaf area or functioning (also possibly on a per shoot basis) and shaded canopies will thus negatively affect berry set. Archer & Strauss (1989) and Smart *et al.* (1989) found that low light intensities have a negative effect on berry set.

Except for the number of clusters and number of berries per cluster, the total yield can also be affected by the berry size. The effect of shade in the canopy on berry size is not very conclusive. Certain authors found that vines with shaded canopies had smaller berries than exposed vines (May & Antcliff, 1963; Reynolds *et al.*, 1986; Archer & Strauss, 1989; Rojas-Lara & Morrison, 1989), while others, such as Bergqvist *et al.* (2001), concluded that the smaller mass of exposed berries may have resulted from the effects of elevated berry temperature on berry cell division or elongation as well as increased fruit transpiration rates and subsequent berry dehydration. These contradictory findings could possibly be the result of rather opposite effects of the shading of the clusters compared to the shading of the leaves. According to Kliewer & Antcliff (1970) shading of the leaves delayed and reduced the berry growth with smaller berries as a result, while covered clusters had heavier berries than the exposed clusters. Shade conditions, especially in the basal part of the canopy, may therefore result in larger berries due to the shading of the clusters themselves.

It had frequently been shown that the best red wines were obtained from grape varieties with small berries (Bidan, 1977), as the most important factors contributing to the originality and quality of wines are localized in the skin. Smaller berries have a larger skin:pulp ratio (Hunter, 1991; Trought, 1996) and therefore higher anthocyanin and phenol concentration (McCarthy, 1996; Gray *et al.*, 1997) and thus better potential for enriching the must (Bravdo & Naor, 1995) to produce a more intense wine (Trought, 1996).

In order to quantify the effect of shoot heterogeneity in a Shiraz/Richter 99 vineyard, certain reproductive growth parameters were measured in order to compare the yield of normally and underdeveloped shoots in shaded as well as in well-exposed canopies.

3. MATERIALS AND METHODS

Experimental vineyard

A seven year old *Vitis vinifera* L. cv. Shiraz, clone SH1A, grafted onto Richter 99 (*Vitis Berlandieri* x *Vitis rupestris*), clone RY2A, vineyard was used for this study. The vineyard is situated at the experimental farm of the Agricultural Research Council (ARC) Infruitec-Nietvoorbij near Stellenbosch in the Western Cape. The vines are spaced 2.75 × 1.5 m on a Glenrosa soil with a western aspect (26° slope) and trained onto a 7-wire lengthened Perold trellising system with movable canopy wires (VSP). Rows were orientated in a North-South direction.

Micro sprinkler irrigation was applied at pea size berry and at véraison. Pest and disease control was applied during the growth season according to the standard program of the ARC.

Experiment design

The experiment was laid out as a completely randomised 2×4×2 factorial design. The three factors were: degree of canopy exposure (well-exposed and shaded canopies); ripening stages (one, three, four and five weeks after véraison); and level of shoot development (normally and underdeveloped shoots). There were three replications for each of the 16 treatment combinations.

Shaded canopies were only shoot positioned and topped, whereas additional suckering and leaf thinning were applied in order to create well-exposed

canopies. Selection of underdeveloped shoots was based on length and comparative lack of lignification at véraison (Fig.1, Chapter 3).

Measurements

Reproductive measurements: All the clusters on the shoots sampled were used. The shoots were randomly selected as described in Chapter 3. Cluster size (length, shoulder width and volume), berry size (mass and volume), number of berries per cluster and the skin:pulp (including seeds) ratio were determined.

Volume measurements were done by water displacement in a measuring cylinder. Berry mass and volume were measured by determining the average of 100 randomly selected berries. The skin:pulp ratio was obtained by dividing skin fresh mass (average of 100 berries) by the mass per berry after the skin fresh mass was subtracted. The mass of the seeds is included in the calculation.

Light intensity measurements: the photosynthetic photon flux density ($W.m^{-2}$) was measured in the vineyard with an ADC portable photosynthesis meter (The Analytical Development Co., England) according to Hunter & Visser (1988). Measurements were taken at 10:00 on the day scheduled (31 January, 8 February and 21 February 2002). Sun leaves in the basal (first three leaves above the bunches) position on the shoot were measured in all the cases whereafter the measurements obtained were converted to molar units per square metre per second ($\mu mol.m^{-2}.s^{-1}$). Three replications were measured.

Relative occurrence of the different shoot types and their percentage fertility: after leaf fall in 2002 the total number of normally and underdeveloped canes were counted on 1054 vines – 527 with shaded and 527 with well-exposed canopies. The number of fertile shoots in each shoot class and the percentage fertility of normally and underdeveloped shoots in shaded and exposed canopies were calculated.

Statistical analyses

Due to the nature of the data, a non-parametric bootstrap analysis was used when it proved to be more practical than factorial ANOVA. The significance of the results was evaluated using 95% confidence intervals. Since only three replications per treatment, tendencies, rather than absolute statistical significances, were discussed. During interpretation of the figures, differences were considered significant when no overlapping of the 95% confidence intervals occurred.

4. RESULTS

Relative occurrence of the different shoot types and their percentage fertility

Relatively more normally developed shoots occurred in the well-exposed compared to the shaded canopies, with a higher fertility percentage in the former. More or less the same percentage infertile, normally developed shoots was found in the shaded and exposed canopies. It seemed as if relatively more underdeveloped shoots occurred in the shaded compared to the exposed canopies, the difference being made up by infertile shoots, since no significant difference in the percentage fertile underdeveloped shoots between the different canopies was observed (Fig. 1)

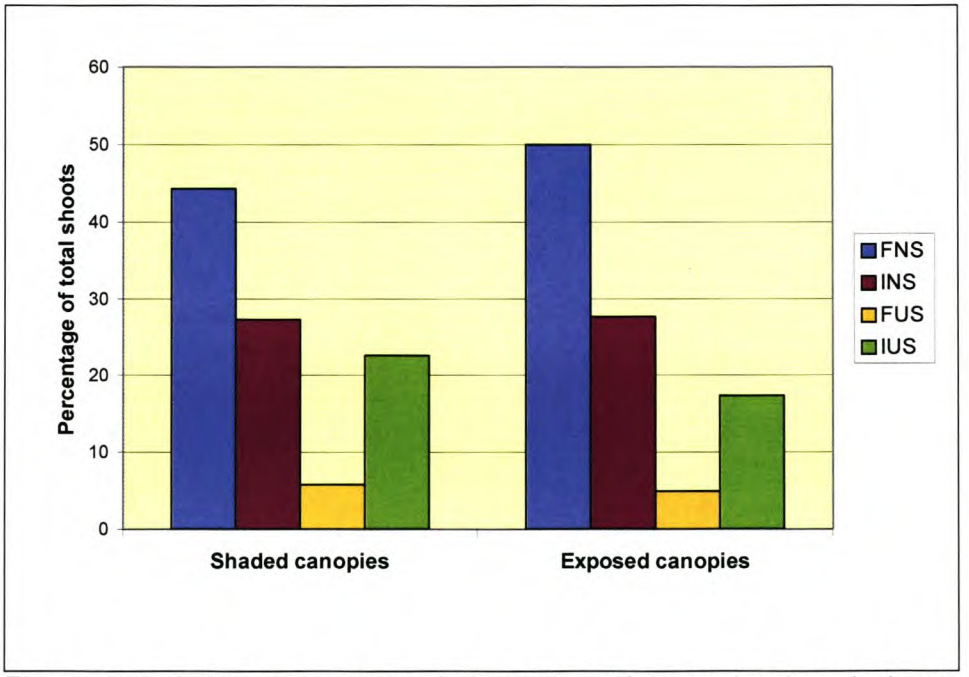

Figure 1 Relative occurrence of normally and underdeveloped shoots and their fertility percentage in well-exposed and shaded canopies (**FNS** – Fertile normal shoots; **INS** – Infertile normal shoots; **FUS** – fertile underdeveloped shoots and **IUS** – Infertile underdeveloped shoots).

Using the total number of shoots in the canopies, as well as the planting density of the vines, an indication of the shoot density in the different canopies was determined. Twenty shoots per metre cordon were calculated for the shaded

canopies, while 17 shoots per metre cordon were found for the well-exposed canopies (data not shown).

Cluster size

Clusters from normally developed shoots were significantly larger than those from underdeveloped shoots, regarding the volume, length and shoulder width ($p \leq 0.01$) (Figs. 2 – 4). The degree of canopy exposure did not seem to affect the cluster size of the normally developed shoots at all, except for the average shoulder width that seemed slightly narrower in the well-exposed canopies (Fig. 4). In the case of the underdeveloped shoots, it seemed as if the clusters in the exposed canopies were a little larger (Fig. 2), although no significant differences in the volume, length and shoulder width were noticed (Figs. 2 - 4).

No significant change in the cluster size in the five weeks following véraison was measured (data not shown).

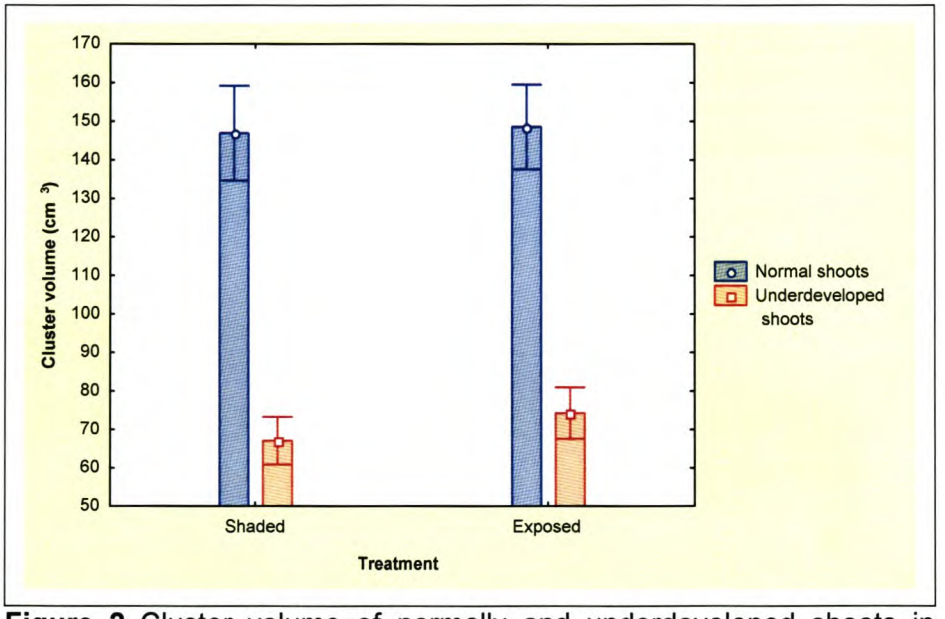

Figure 2 Cluster volume of normally and underdeveloped shoots in shaded and well-exposed canopies. Error bars indicate 95% confidence intervals.

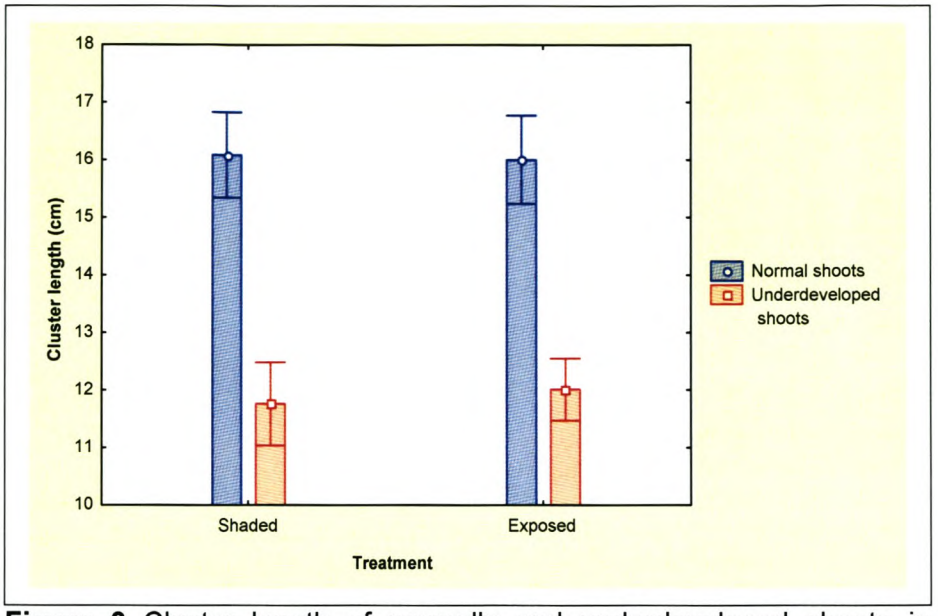

Figure 3 Cluster length of normally and underdeveloped shoots in shaded and well-exposed canopies. Error bars indicate 95% confidence intervals.

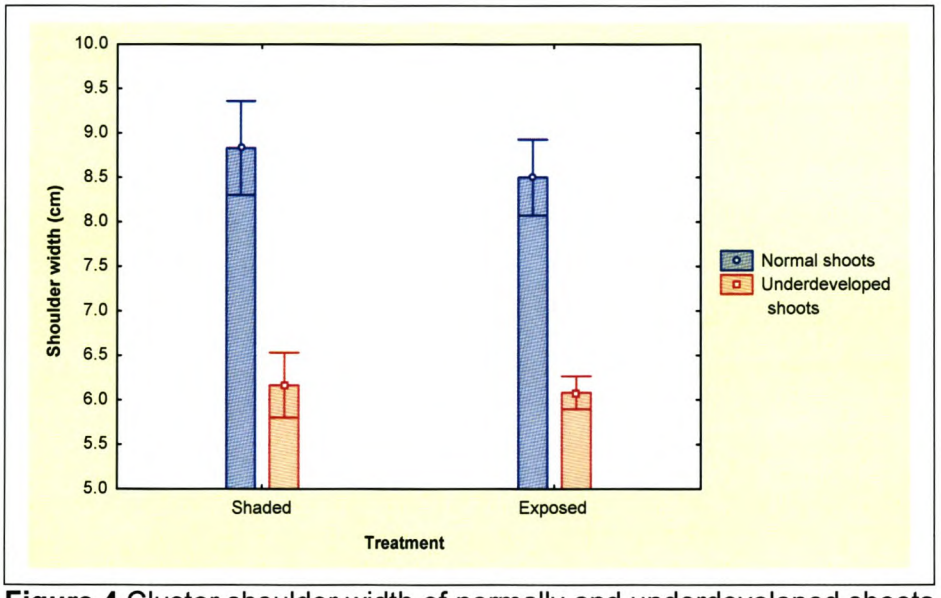

Figure 4 Cluster shoulder width of normally and underdeveloped shoots in shaded and well-exposed canopies. Error bars indicate 95% confidence intervals.

Berries per cluster

As could well be expected, the number of berries per cluster did not change in the five weeks after véraison (data not shown). Significantly more berries were found on clusters from normal shoots compared to underdeveloped shoots ($p \leq 0.01$). Although the degree of canopy exposure did not seem to affect the berry set of normal shoots, more berries seemed to be found in clusters from underdeveloped shoots in the well-exposed than the shaded canopies, albeit not statistically significant (Fig. 5).

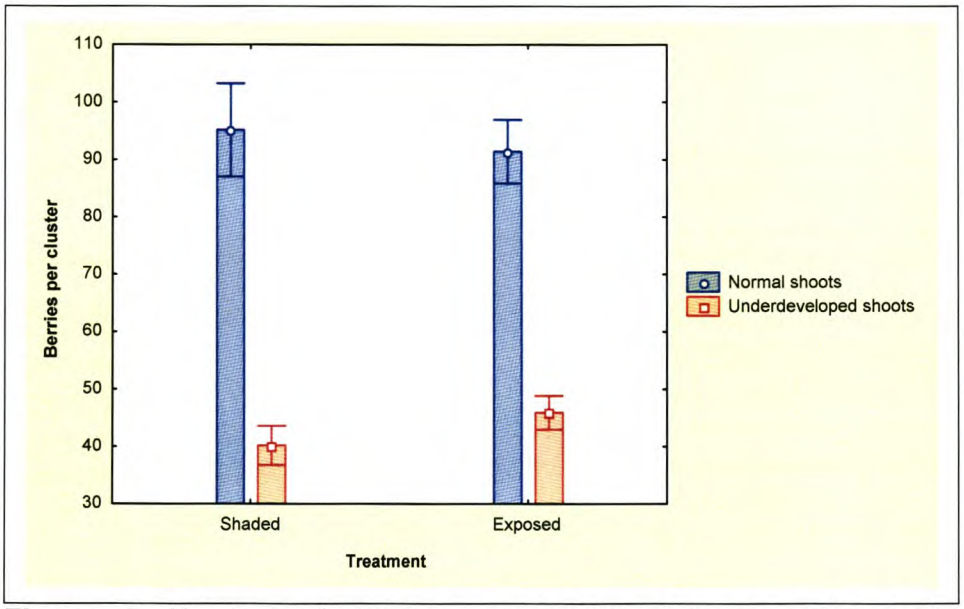

Figure 5 Number of berries per cluster from normally and underdeveloped shoots in shaded and well-exposed canopies. Error bars indicate 95% confidence intervals (bootstrap analysis).

Berry size

Up to three weeks after véraison, no significant difference in the berry mass (Fig. 6) and volume (Fig. 7) of clusters on normal shoots between shaded and well-exposed canopies was found. Between three and five weeks after véraison the berry size in the shaded canopies decreased more sharply than in the exposed canopies. Thus, regarding normally developed shoots at five weeks after véraison, berries with a higher mass and volume seemed to occur in well-exposed compared to shaded canopies.

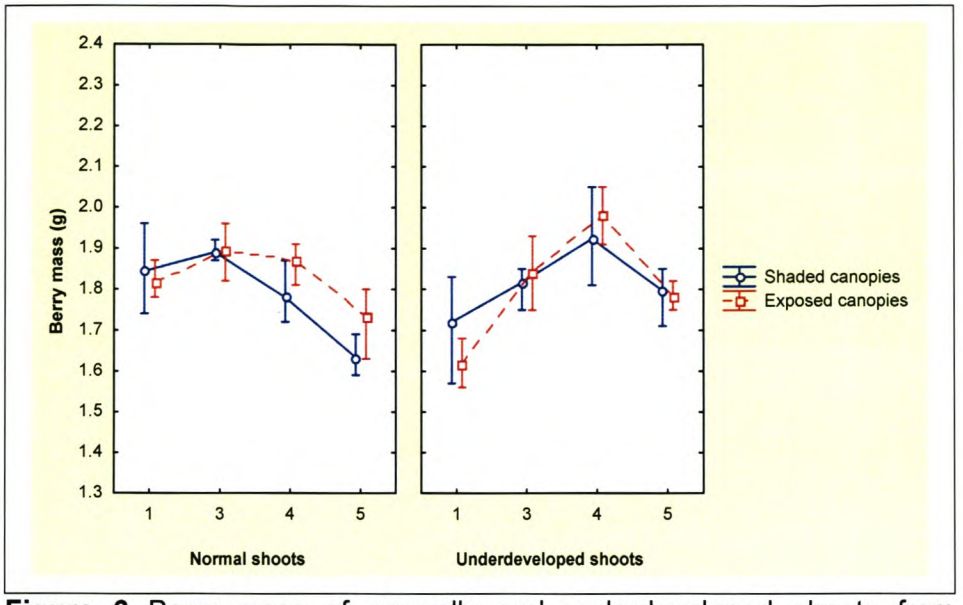

Figure 6 Berry mass of normally and underdeveloped shoots from shaded and well-exposed canopies at one, three, four and five weeks after véraison. Error bars indicate 95% confidence intervals (bootstrap analysis).

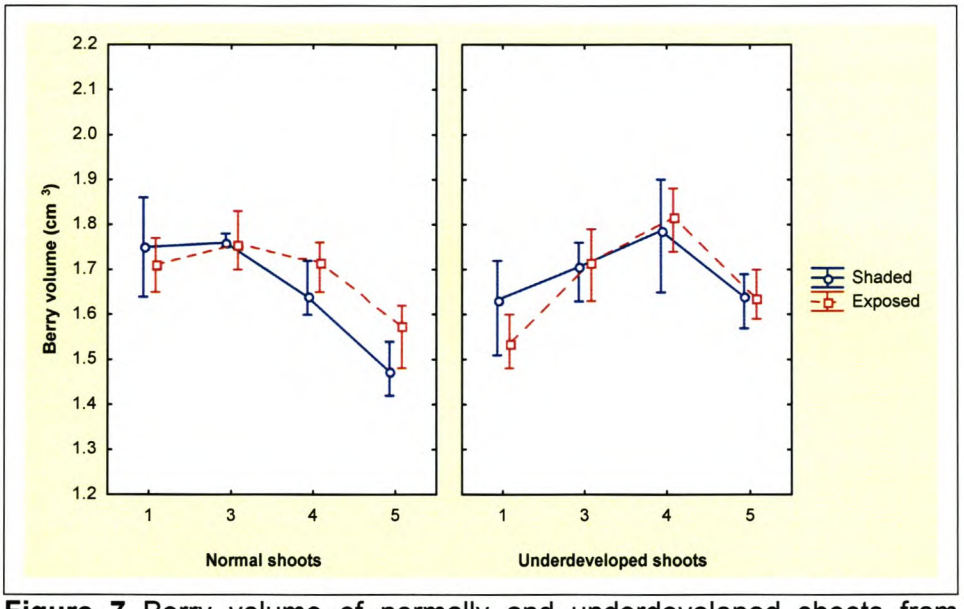

Figure 7 Berry volume of normally and underdeveloped shoots from shaded and well-exposed canopies at one, three, four and five weeks after véraison. Error bars indicate 95% confidence intervals (bootstrap analysis).

The degree of canopy exposure had a smaller effect on the berry size of underdeveloped shoots. Although the berry mass (Fig. 6) and volume (Fig. 7) tended to be lower in the exposed canopies one week after véraison, it was not significant. During the following four weeks no difference in berry size of underdeveloped shoots was found between the canopy treatments.

The patterns of berry development were different between the two types of shoots: berry development in normal shoots already peaked three weeks after véraison, whereas that of underdeveloped shoots peaked only after four weeks.

The mass (Fig. 8) and volume (Fig. 9) of berries from normally developed shoots increased up to three weeks after véraison, whereafter the berry size decreased. In comparison, the berry mass and volume from underdeveloped shoots only started to decrease in the fifth week after véraison. In the first week after véraison the berries from the normally developed shoots were somewhat larger than those from undeveloped shoots. After two more weeks the berries from the normal shoots were still larger, the difference however much smaller. At four and five weeks after véraison it was found that grape berries from underdeveloped shoots were on average larger in mass and volume than those from normally developed shoots.

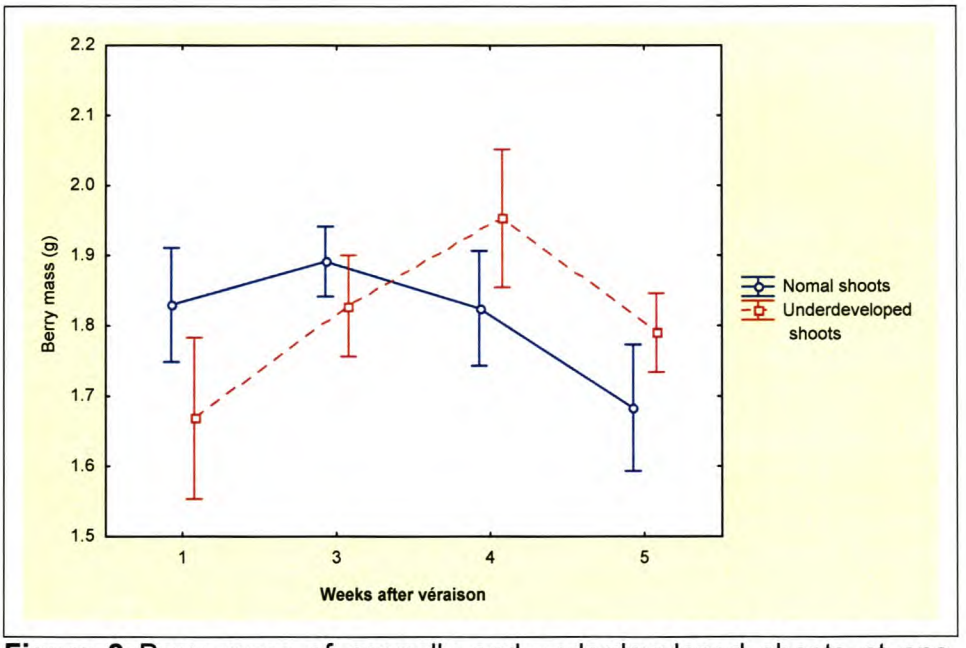

Figure 8 Berry mass of normally and underdeveloped shoots at one, three, four and five weeks after véraison. Error bars indicate 95% confidence intervals.

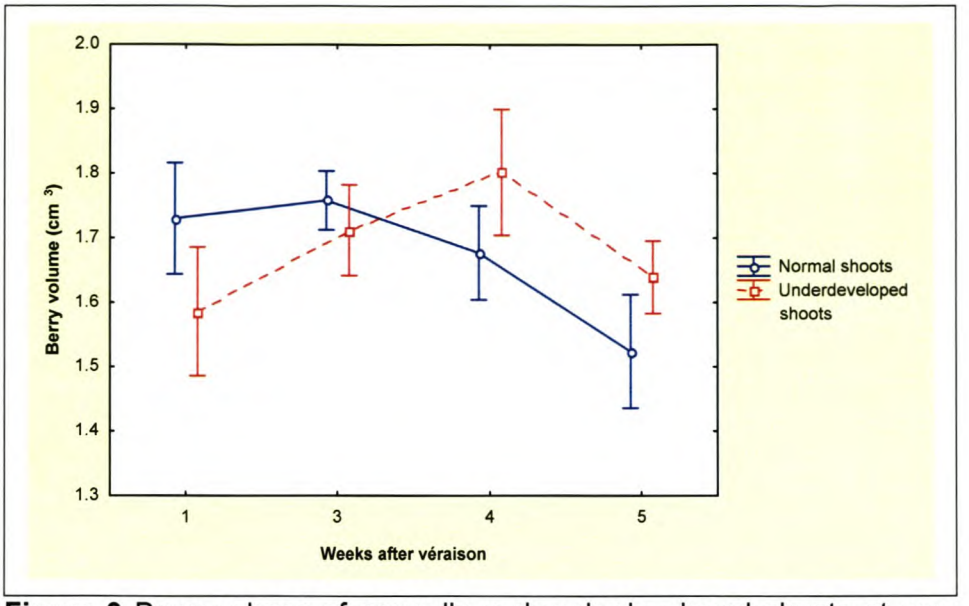

Figure 9 Berry volume of normally and underdeveloped shoots at one, three, four and five weeks after véraison. Error bars indicate 95% confidence intervals.

Skin:pulp ratio of the berries

The skin:pulp ratio of all the grape berries increased during the five weeks after véraison (Figs. 10 - 12).

When the degree of canopy exposure was considered as the main treatment, no statistical significant difference during any ripening stage was found between the skin:pulp ratio of the berries in the shaded and exposed canopies ($p \leq 0.44$) (Fig. 10). From four to five weeks after véraison, a smaller variation in the ratio occurred for berries in the more exposed canopies.

Regarding the normal shoots, no difference in the skin:pulp ratio was found between the shaded and exposed canopies in the first four weeks after véraison. In the fifth week it seemed as if the berries in the shaded canopies had a higher average ratio, although the difference was not significant. A smaller variation was found at the same time between the berries in the exposed canopies (Fig. 11).

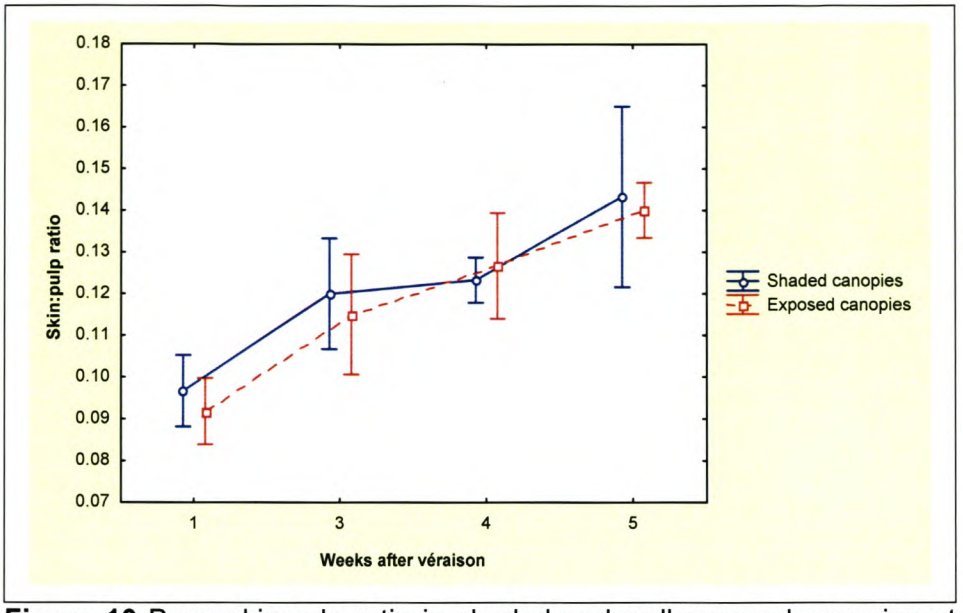

Figure 10 Berry skin:pulp ratio in shaded and well-exposed canopies at one, three, four and five weeks after véraison. Error bars indicate 95% confidence intervals.

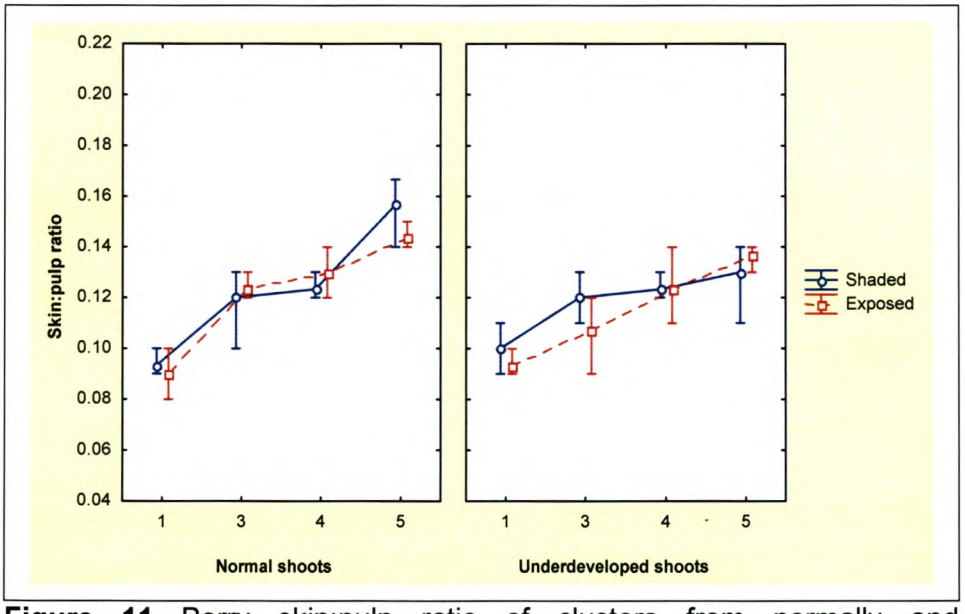

Figure 11 Berry skin:pulp ratio of clusters from normally and underdeveloped shoots in shaded and well-exposed canopies at one, three, four and five weeks after véraison. Error bars indicate 95% confidence intervals (bootstrap analysis).

The skin:pulp ratio of berries from underdeveloped shoots tended to be smaller in the exposed canopies during the first three weeks after véraison, albeit not statistically significant. At four and five weeks no difference between the canopy treatments was found, although there seemed to be less variation in the ratio after five weeks in the well-exposed canopies (Fig. 11).

Although no significant difference was found during any ripening stage, it seemed as if the skin:pulp ratio of the berries from normal shoots tended to be higher than from the underdeveloped shoots from the second week after véraison onwards (Fig. 12).

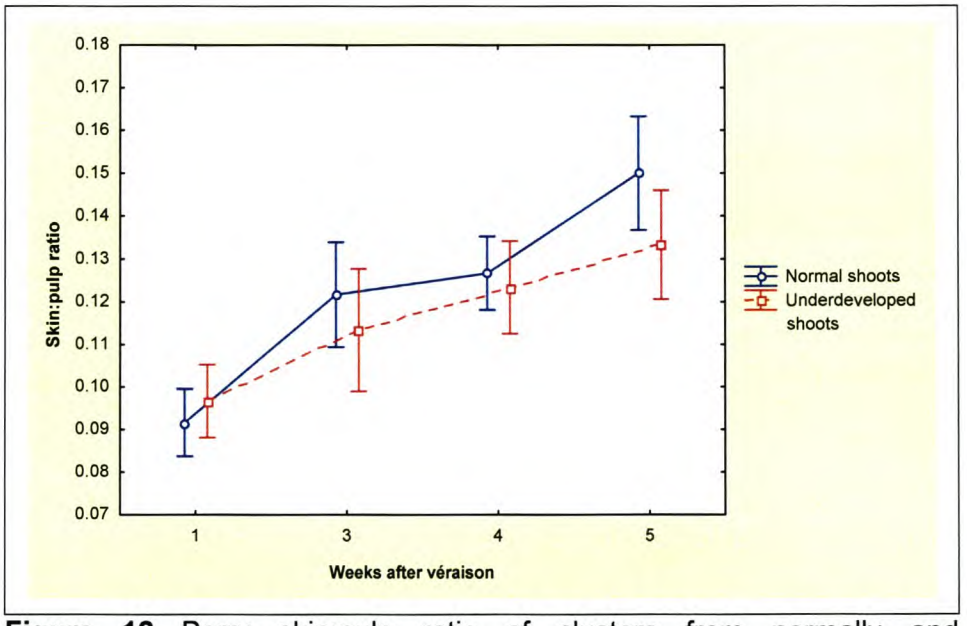

Figure 12 Berry skin:pulp ratio of clusters from normally and underdeveloped shoots at one, three, four and five weeks after véraison. Error bars indicate 95% confidence intervals.

5. DISCUSSION

Vegetative characteristics of the different canopy treatments

When the density of the different canopies were determined, 17 shoots per metre cordon were counted for the canopies in which additional suckering and leaf removal were executed compared to the 20 shoots per metre cordon for the other canopies. According to Archer (2002, personal communication) 12 shoots per metre cordon in cooler areas and 18 shoots in warmer areas are considered as optimal for quality grape production. It may thus be that the microclimate in

the denser canopies was not conducive to optimal cluster development and ripening, which may be a contributing factor if differences in grape composition and quality between the more exposed and more shaded canopies are found.

A lower percentage normally developed, fertile shoots occurred in shaded canopies, which were only shoot positioned and topped, than in well-exposed canopies that were created by additional suckering and leaf removal.

Quinlan & Weaver (1970) found that that removal of a sink increased the availability of assimilates to adjacent sinks. By decreasing the level of available assimilates within a shoot, they also created a compensatory movement of photosynthetates to the particular shoot. The higher total shoot number in shaded canopies (as a result of the omission of suckering) increased the number of vegetative sinks of these vines. It may therefore be assumed that the flow of assimilates to each individual shoot on the vine would have been reduced, with a resultant decrease in vegetative growth. This could be a possible explanation for the lower percentage (and lower number) of normal shoots found in the shaded than in the well-exposed canopies. It therefore seemed as if canopy management stimulated more uniform growth in the canopies.

It seemed as if the above scenario is also possible in the beginning of the growth season regarding reserve distribution, which would have resulted in a decreased initial vegetative growth. This could be a reason why underdeveloped shoots could mostly already be identified rather early in the season.

The higher occurrence of underdeveloped shoots noted in the shaded canopies is in accordance with Smart (1988) who found a large proportion of short shoots in dense canopy interiors. Only about 20 percent of these underdeveloped shoots were found to be fertile (data not shown). Peterson & Smart (1975), however, mentioned that short shoots may have insufficient leaf area to adequately ripen their fruit. It was found that underdeveloped shoots had a smaller primary as well as secondary leaf area than normally developed shoots, due to smaller primary leaves and fewer and smaller secondary leaves (Chapter 3). A proper relationship between the active leaves and the clusters per individual shoot is important. It is accepted that 10 cm^2 to 12 cm^2 leaf area is generally required to ripen one gram of fruit (Hunter & Visser, 1990, and references therein). In the grapevine it is seen as over-cropping when supply is inadequate to meet the demand of the sink tissues (Bravdo & Naor, 1995). This is also possible on a per shoot basis, which could be an explanation why Koblet

(1977) found that grapes from shorter shoots showed a slight reduction in sugar concentration as well as a reduction in colour and phenols.

Although all shoots exported their products partially to adjacent shoots, it was found that short shoots imported more assimilate than normally developed shoots in order to ripen their clusters (Koblet, 1977). The assumption could thus be made that the presence of short, fertile shoots could be responsible for a decrease in the grape quality of the other, stronger shoots from the same vine and thus affect the quality of the total crop. This also has further implications when grapes from such shoots are mixed together with those of normal shoots when harvesting takes place.

Since a higher total number of shoots (data not shown), less normally developed and more underdeveloped shoots were found in shaded than in well-exposed canopies (Fig. 1), shoot heterogeneity existed to a larger degree in the former. According to Jackson & Lombard (1993), asynchronous ripening may be enhanced by the varying leaf area:fruit ratio of individual shoots. While comparing two different vineyards, Long (1987) found that the vineyard that consistently produced better flavoured wine had less variability in ripeness. In accordance, Smart *et al.* (1990) stated that high quality wines probably resulted from processing fruit of relatively similar composition. Different shoot lengths in a vine would thus lessen the overall quality of the yield (Archer, 2001), while equality in shoot growth seems important for the production of homogeneous, top quality grapes.

Apart from the possible decrease in the overall quality of the yield, the presence of a large number of underdeveloped shoots in the canopy interior (Smart, 1988) will most certainly affect the sunlight penetration to the basal part of dense canopies and thus also the size of the yield. According to Archer & Strauss (1989) low light intensities in canopy interiors resulted in the significant decrease in berry mass, cluster mass and the yield per vine. It was ascribed to unfavourable microclimatic conditions that were detrimental to bud fertility and berry set.

The lower PPFD levels received by the basal leaves in the shaded canopies (Chapter 4) could also have affected the fertility of the basal buds, since Archer (1988) and Hunter (1991) found a reduction in bud fertility due to low light intensities. This could be a partial explanation for the lower fertility percentage of especially the normally developed shoots in the shaded canopies.

The difference in fertility between the underdeveloped shoots from the shaded and well-exposed canopies was not as apparent, probably because of the large variation in PPFD received by these shoots. Also, they received lower levels of radiation than normally developed shoots in the well-exposed as well as in the shaded canopies, which may indicate that underdeveloped shoots tended to develop in the canopy interior (in accordance with the findings of Smart, 1988). Another probable explanation for the lower PPFD received by the underdeveloped shoots is that these shoots were pushed to the canopy interior during shoot positioning, because they were too short to be accommodated by the canopy wires. The larger leaves (and possibly the thicker shoots as well) of the normally developed shoots (Chapter 3) most probably had a higher overshadowing effect on underdeveloped shoots towards the canopy interior. Whatever the reason, the lower exposure of the underdeveloped shoots to PPFD could have been an important reason for their lower fertility in comparison to that of the normally developed shoots.

According to Winkler *et al.* (1974), Lavee *et al.* (1967) showed that a certain amount of leaf area, which may differ between cultivars, is needed for the induction of fruit primordia in grape buds. It is thus possible that insufficient leaf area could have been a limiting factor to the fertility of underdeveloped shoots.

The existence and importance of certain balances in the vine is well known in the literature as well in practice. It is very important to maintain the balance between vegetative growth, reproductive growth and reserve accumulation during the cultivation of grapevines (Hunter, 1991). Scienza *et al.* (1995) found the balance between yield and vegetative growth useful to explain variation in wine quality. These balances also played an important part in the formation of fruit buds in the vine. Winkler (1929), according to Winkler *et al.* (1974), found that methods that excessively increased the vigour of shoots led to the decrease in bud fruitfulness, while Thomas & Barnard (1937) apparently observed the same effect on fruitfulness while working on vines with a below-average to weak growth. They found that the percentage of starch in the annual wood is closely associated with fruit bud formation.

It is therefore quite reasonable to expect that the fertility of too vigorous or underdeveloped shoots will be lower than normally developed shoots with a moderate vigour. In addition to the extent of reserve accumulation in the permanent wood, such as the roots and trunk, the amount of starch accumulation

in the spurs during the previous season may also be of great importance on a per shoot basis.

Cluster size

Although the bud fertility is already determined in the previous growth season during the induction phase (Swanepoel & Archer, 1988), the actual size of the clusters is not established during that phase, as it is mostly predetermined by the genetics of the cultivar. Despite that, variation in the cluster size in a specific vineyard block normally occurs, which indicates that there are other factors that also affect the cluster size.

Since no significant change in the cluster size (length, shoulder width and volume) was noticed in the five weeks after véraison, it may be that the cluster size is affected before véraison during the vegetative growth phase of the shoots. The degree of canopy exposure does not seem to be an important factor in the determination of the cluster size, since no significant difference in the PPFD between the shaded and well-exposed canopies was found just after véraison (Chapter 4). It was therefore assumed that during the shoot growth phase no significant difference in the level of exposure existed between the canopies.

Clusters on the normally developed shoots were significantly larger than those on underdeveloped shoots, regarding the length, shoulder width and volume (Figs. 2 - 4). According to Winkler *et al.* (1974) flower clusters of shoots on strong, well-ripened spurs will be more advanced in development than those on spurs that are weak. The weaker clusters seldom overcome these differences in development. It was noticed that normally developed shoots mostly originate from strong, well-ripened spurs, while weaker spurs commonly gave rise to weak, underdeveloped shoots. This explains the difference in cluster size between normally and underdeveloped shoots.

Winkler *et al.* (1974) further found that larger clusters occurred on vines carrying a balanced crop compared to vines with an excessive crop, which illustrates the importance of nutrition on the development of flower clusters after the start of new growth. Once again, this statement was tested on a per shoot basis. It was found that in exposed canopies an average of 9 cm^2 leaf area was available on underdeveloped shoots to ripen one gram of grape berries, compared to the 13 cm^2 of normal shoots (data not shown). Since 12 cm^2 is normally considered as the norm for balanced vegetative:reproductive growth (Hunter, 1991), it could be stated that normally developed shoots carried a normal crop, while the crop

load of underdeveloped shoots was excessive in relation to their fruit ripening potential. This may also be the reason for the smaller clusters found on underdeveloped shoots compared to normal shoots.

Berries per cluster

The number of berries per cluster can be directly linked to the berry set phase after flowering. If berry set is negatively affected, it will lead to fewer berries per cluster with the resultant decrease in yield.

The shoot tips and parent vine were found to be more powerful sinks than the clusters during flower development, but not during berry set (Hale & Weaver, 1962). Hunter (1991) found the cluster to be the strongest sink for assimilates at berry set, which is an indication of the importance of this phase for the vine. According to Kriedemann (1977), May *et al.* (1973) stated that poor fruit set is a primary limitation to yield in the grapevine. Therefore it should as far as possible be ensured that any factor that can detrimentally affect berry set is avoided.

Winkler *et al.* (1974) stated that two schools of thought exist as to which factors are responsible for berry set in grapevines. It can either occur due to the effect of growth regulators, or it can be regulated by the supply of organic nutrients. It seemed as if there exist stronger evidence for the latter option. Keller & Hrazdina (1996) found that a low nitrogen supply during bloom affected berry set negatively, while Caspari & Lang (1996) linked berry set with the carbohydrate supply to the clusters. Any factors and/or practices that will decrease the movement of organic nutrients to the clusters, such as unbalanced vegetative:reproductive growth ratio, inadequate functioning leaf area due to extreme temperatures, water deficiency or shaded canopies, will detrimentally affect berry set.

More berries per cluster were found for the underdeveloped shoots in the exposed compared to the shaded canopies (Fig. 5). It could be explained by the possible better cluster nutrition in the exposed canopies, since a little better light penetration was measured in the latter (Chapter 4). This is in accordance with the findings of Archer & Strauss (1989) and Smart *et al.* (1989) who found that low light intensities in the canopy had a negative effect on berry set.

Higher levels of PPFD was constantly received by the basal leaves of normally compared to underdeveloped shoots, even when normal shoots in shaded canopies was compared to the underdeveloped shoots in the well-exposed

canopies (Chapter 4). The significantly higher number of berries per cluster found for the normal shoots (Fig. 5) could thus easily be explained. However, the difference in the levels of PPFD received by the leaves of the different shoots did not differ to such an extent that it justified the degree of difference in berry set between the shoots. Therefore the relationship between the amount of radiation received in the basal part of the canopy and berry set was not linear. There seems to exist a certain range in the radiation flux density that has a higher impact on berry set. Higher levels of PPFD would not increase berry set to the same degree, while lower PPFD would affect berry set detrimentally.

Since the degree of canopy exposure did not affect the normal shoots to the same extent as underdeveloped shoots (Fig. 5), it was assumed that the optimal light intensity for berry set was reached in both canopies and that other factors were also prevalent in the regulation of berry set.

Keller & Hrazdina (1996) mentioned the possible effect of low nitrogen supply on inflorescence necrosis and the resultant poor berry set. Since the normally and underdeveloped shoots used for measurements were situated on the same vines in a single block with no variation in soil type or fertilization practices, this possibility can probably be ruled out. Another possible factor is the carbohydrate supply to the clusters as mentioned by Caspari & Lang (1996). Although no symptoms similar to EBSN was noticed, it may be that a lower carbohydrate supply may have a detrimental effect on berry set without causing any visible symptoms. This would also explain the effect of the more shaded canopies on the degree of berry set, since low light conditions lead to a decrease in photosynthetic activity of leaves (Kriedemann, 1977) and thus also the amount of carbohydrates available to the clusters.

As already mentioned, in most cases the underdeveloped shoots and normal shoots were already distinguished rather early in the season. It could thus naturally be assumed that during berry set the normally developed shoots were longer with a larger leaf area than the underdeveloped shoots, as was found to be the case later in the growth season (Chapter 3). The larger leaf area would most probably have resulted in a better carbohydrate supply to the clusters, due to a higher total photosynthetic activity per shoot. The decreased berry set found with underdeveloped shoots could thus have been due to the inadequate carbohydrate supply by the smaller active leaf area of the specific shoots.

According to Quinlan & Weaver (1970) and Koblet (1977) assimilates are interchanged between adjacent shoots, while sucrose imported to the cluster can originate in either adjacent shoots or from the rest of the permanent vine structure (Hunter & Ruffner, 2001). Ho (1988) found that import rate of assimilates into a sink is regulated by the metabolic activity of the sink. Since it was found that clusters on normally developed shoots were significantly larger than those on underdeveloped shoots, the ability to import assimilates (and thus the sink strength) was probably also higher. Therefore, even if the clusters can receive assimilates from other sources in addition to that produced by the shoots themselves, the clusters on the normal shoots would still receive a larger percentage of the nutrient pool compared to the underdeveloped shoots. It could thus be stated that the clusters on the underdeveloped shoots receive too little organic nutrients for optimal berry set.

Berry size and skin:pulp ratio

The grape berry is non-climacteric with a double sigmoid growth curve (Hunter, 1991). According to Pratt (1988) the increase in berry mass can be divided into three phases: a period of rapid growth until the seeds reach their mature size; a period of slow growth ending with the beginning of véraison; and a period of rapid growth ending in maturity.

The first rapid growth phase is mainly due to high cell division activity (Staudt *et al.*, 1986), while the second rapid growth phase is the result of extensive cell expansion (Alleweldt, 1977). During the latter phase carbohydrates accumulate in the berries (Alleweldt, 1977), mainly as glucose and fructose. Ollat & Gaudillère (1997) also found an increase in carbon import in this phase which is also known as the ripening phase, since it is normally associated with softening, colouring and sweetening (Hunter, 1991).

In the case of ripened and over-ripened berries it was found that several solutes in the berry flesh was concentrated due to water loss (Coombe, 1987). This would explain the loss in mass and volume of berries from normally and underdeveloped shoots three and five weeks after véraison, respectively (Figs. 6 - 9).

Since only the cells formed during the first growth phase of cell division are available for cell enlargement during the second growth phase, it stands to reason that the skin:pulp ratio will decrease as berry enlargement proceeds.

This, however, did not seem to be true in this case, since the skin:pulp ratio continuously increased from the first to the fifth week after véraison, in the case of the normally and underdeveloped shoots in shaded and well-exposed canopies (Figs. 10 - 12). It was mainly ascribed to the decrease in berry size (especially regarding the normal shoots) during this time (Figs. 6 - 9).

No statistically significant effect of canopy exposure on the berry size was found for the normal shoots (Figs. 6 & 7), although it seemed as if the berries in the well-exposed canopies, especially during the later stages of berry ripening, tended to be a little larger than those in the shaded canopies. In the literature the effect of shade in the canopy on the berry size is not very conclusive. These contradictory findings could possibly be the result of rather opposite effects of the shading of the clusters compared to the shading of the leaves. According to Kliewer & Antcliff (1970) shading of the leaves delayed and reduced the berry growth with smaller berries as a result, while covered clusters had heavier berries than the exposed clusters.

It is thus possible that the leaves of the normal shoots in the shaded canopies were not exposed to sufficient sunlight for optimal photosynthetic activity in the grape ripening period. Lower PPFD levels were measured with normal shoots in shaded canopies in the third and fifth week after véraison, the latter being statistically significant (Chapter 4). But since the average light intensity in the shaded canopies was still about 1000 $\mu mol.m^{-2}.s^{-1}$, it was not considered as an inhibiting factor to photosynthesis. Despite that, it seemed like the photosynthetic activity of the leaves from normal shoots in the shaded canopies was significant lower than in the exposed canopies in the fifth week after véraison (Chapter 4). Therefore the process of carbohydrate accumulation during the second rapid growth phase of the grape berry was probably impaired in the shaded canopies, which will explain the smaller berries found.

During the ripening stage of Shiraz, two different processes affect berry size, namely the cell expansion due to water uptake and carbohydrate accumulation (Alleweldt, 1977) and berry shrinkage due to water loss from the berries (Iland & Coombe, 1988; Rogiers *et al.*, 2000). It has already been established that the former process probably did not occur optimally in the berries of the normal shoots in the shaded canopies, but the significant decrease in berry mass and volume between four and five weeks after véraison seemed to indicate that the latter process still continued (Fig. 7). The berry size of the normal shoots in the exposed canopies did not appear to decrease at the same rate (although the

decrease was still statistically significant) as in the shaded canopies, since carbohydrate accumulation and thus berry growth still occurred simultaneously to the water loss.

Since anthocyanins and phenols, which are important factors contributing to the quality of the wine, are localized in the skin (Bidan, 1977), smaller berries which have a higher skin:pulp ratio than larger berries (Hunter 1991; Trought, 1996) will have a better potential for enriching the must (Bravdo & Naor, 1995) to produce a more intense wine (Trought, 1996). Wines made from smaller berries are normally more highly coloured and flavoursome (McCarthy, 1996) compared to those made from larger berries. Since the berries of the normal shoots in the shaded canopies were found to be smaller than those in the exposed canopies (Figs. 6 & 7) with a higher skin:pulp ratio five weeks after véraison (Fig. 11), it seemed as if these berries had a higher potential for quality wine production than the berries in the well-exposed canopies.

However, as already discussed, the smaller size of the berries in the shade is probably due to impaired carbohydrate accumulation in the second rapid growth phase as a result of decreased photosynthetic activity under low light intensities rather than the concentration of solutes through water loss. Therefore, despite the smaller berry size and higher skin:pulp ratio of the berries in the shade, it is not expected that these berries will be higher in quality nor produce better quality wines than the better exposed berries.

The degree of canopy exposure hardly seemed to affect the berry size on the underdeveloped shoots, since the berry mass or volume did not differ significantly in the five weeks after véraison. No statistically significant difference was found between the levels of PPFD received by the basal leaves of underdeveloped shoots in shaded and well-exposed canopies, even though the photosynthetic activity of the leaves in the exposed canopies was found to be significant higher than that in the shaded canopies five weeks after véraison (Chapter 4). The clusters of underdeveloped shoots in the exposed canopies were considered to be larger sinks than those in the shaded canopies, due to the larger number of berries per cluster (Fig. 5). The higher levels of assimilates produced by the leaves in the well-exposed canopies were thus still used for berry growth and ripening, since no significant difference in the individual berry size between the canopies was noticed.

No difference in the skin:pulp ratio between the berries of underdeveloped shoots in the shaded and exposed canopies was found. Since no physical differences (such as berry size or skin:pulp ratio), which could indicate possible difference in the berry quality, were found between the shaded and exposed canopies, no grape quality deductions can be made without further berry analyses.

Although the berry size of the normally developed shoots was larger during the first three weeks after véraison, the berries were found to be smaller than those on underdeveloped shoots five weeks after véraison due to earlier shrinkage of the berries (Figs. 8 & 9). The larger skin:pulp ratio of the normal shoots compared to the underdeveloped shoots (Fig. 12) is in accordance with Hunter (1991) and Trought (1996) who stated that smaller berries have a larger skin:pulp ratio than larger berries. Hence it seems as if the berries from the normal shoots could have a higher potential for the production of quality wine, since the smaller berries and higher skin:pulp ratio will probably induce better colour and phenol extraction (McCarthy, 1996).

It rather seemed as if the normal ripening curve of the berries was somewhat delayed in the underdeveloped shoots, since the decrease in berry mass and volume started approximately one week later than in the normal shoots (Figs. 8 & 9). The maintenance of the balance between vegetative and reproductive growth in the grapevine is very important (Hunter, 1991). Scienza *et al.* (1995, and references therein) linked decreased must and wine quality with an imbalanced source:sink ratio in the vine. Excessive vigour and under-cropping normally result in a decreased yield and wine quality, due to the strong competition of the growing shoot tips for carbohydrates (Boulton *et al.*, 1998). Canopy shade of vigorous vines was associated with delayed grape maturation (Archer, 1988; Smart *et al.*, 1988; Smart *et al.*, 1989; Keller & Hrazdina, 1996), while Rojas-Lara & Morrison (1989) found that shaded canopies led to delayed berry growth and ripening. Optimum ripening also seemed to be inhibited (Archer, 1988).

On the other hand, too high yield (and thus over-cropping) could decrease the quality (Jackson & Lombard, 1993) since the photosynthetic capacity of the vine would be insufficient to adequately ripen the clusters. Either the harvest date will be significantly delayed, or the grapes will never reach the desired ripeness levels (Boulton *et al.*, 1998). Underdeveloped shoots could possibly be seen as over-cropped, since their leaf area per shoot as well as the physiological activity of the leaves could be insufficient to adequately ripen their clusters

(Chapters 3 & 4). An unbalanced source:sink ratio in these shoots would also explain the apparent delay in the berry ripening curves of underdeveloped compared to normally developed shoots (Figs. 8 & 9).

Therefore it is expected that the yield from the normal shoots will be better ripened and produce better quality wines than that from the underdeveloped shoots. To what extent the composition of the berries differs, should be clarified after further analyses.

6. CONCLUSIONS

A higher number of total shoots and thus more shoots per metre cordon was found in the shaded than in the exposed canopies. The difference in shoot number was ascribed to the suckering procedure that was carried out in the latter. The lower percentage normally developed shoots and higher percentage underdeveloped shoots in the shaded compared to exposed canopies was explained by the reduced translocation to each individual shoot due to the higher shoot number. Because of the constantly lower levels of PPFD received by the underdeveloped compared to the normal shoots in both the shaded and well-exposed canopies, it was concluded that the underdeveloped shoots were probably situated more to the canopy interior. The lower PPFD received by the basal leaves of underdeveloped shoots could have been the reason for the low level of fertility found in these shoots. The possibility of insufficient leaf area per underdeveloped shoot for the induction of fruit primordia was also explored, as well as the possible effect of sub-optimal starch accumulation in the spurs during the previous growth season. The position of the underdeveloped shoots in the canopies also probably explains the lower percentage fertility found for the normal shoots in the shaded canopies. Interior canopy shade is known to decrease the yield due to the detrimental effect on bud fertility and berry set as well as berry growth and ripening. It was found that shoot heterogeneity existed to a greater extent in the shaded than exposed canopies. Therefore asynchronous ripening with more variation in berry composition is expected for these canopies. Since the quality of the wine had been associated with the uniformity of berry ripening, the wines made from the clusters in the shaded canopies are likely to be of lower quality.

Cluster size is probably affected before véraison during the vegetative growth phase of the shoots and therefore the degree of canopy exposure did not seem

to affect the cluster size significantly. The larger clusters found on normally than underdeveloped shoots were partly explained by the difference in degree of spur development and ripening, since underdeveloped shoots were commonly found to grow from weaker spurs. Another reason is that the crop load of underdeveloped shoots could be excessive in relation to their fruit ripening potential. This was probably compensated by a decrease in the cluster size.

The degree of canopy exposure seemed to have a larger effect on berry set of the underdeveloped than the normal shoots. The higher number of berries per cluster found for the underdeveloped shoots in the exposed canopies was explained by the better cluster nutrition due to the improved light penetration inside the canopies. The clusters from normal shoots had significantly more berries per cluster than those from underdeveloped shoots. The higher levels of PPFD received by the normal shoots only partly explained this, since the light intensity received did not differ to the same extent as the berry number. There seemed to exist a certain range in the radiation flux density that is optimal for berry set. Other factors such as the carbohydrate supply to the clusters were also considered, since a connection between the carbohydrate supply and berry set has already been established. The larger leaf area found with normal shoots as well as the stronger sink strength of their larger clusters would have resulted in a larger carbohydrate flow to the clusters of the normal shoots compared to those on the underdeveloped shoots – from the shoots themselves due to the larger leaf area as well as from other vine structures due to their higher ability to import assimilates. The better carbohydrate supply thus increased the berry set of the clusters on the normal shoots.

The berry size of the normal shoots did not differ significantly between the different canopies, although it seemed as if the berries in the exposed canopies tended to be a little larger than those in shaded canopies close to ripeness. It was attributed to the lower photosynthetic activity found for the leaves in the shaded canopies that impaired the carbohydrate accumulation during the second rapid growth phase of the berries and resulted in the smaller berries found. Despite the smaller berry size and higher skin:pulp ratio of the berries in the shade, better composition and quality than the berries in the exposed canopies were thus not expected. The degree of canopy exposure did not affect the berry size of the underdeveloped shoots. The significantly higher photosynthetic activity measured in the leaves from the exposed canopies did not result in larger berries, but rather in more berries per cluster. It further seemed as if the normal ripening curve of the berries was delayed for the underdeveloped compared to

the normal shoots. This is similar to the effect of over-cropping, where the photosynthetic capacity is insufficient to adequately ripen the clusters. The delayed ripening together with the larger berries and smaller skin:pulp ratio found, led to the deduction that berries from the normal shoots will be better ripened and produce wine with more intense flavour and colour than those from underdeveloped shoots.

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CHAPTER 7

RESEARCH RESULTS

THE EFFECT OF SHOOT HETEROGENEITY ON GRAPE COMPOSITION OF SHIRAZ/RICHTER 99 GRAPEVINES

1. ABSTRACT

In this study the physiological potential of normally and underdeveloped shoots were compared in an attempt to quantify the effect of shoot heterogeneity in a Shiraz/Richter 99 vineyard. The field trial was performed in the Stellenbosch area, Western Cape, South Africa. Comparisons based on certain berry composition parameters were made between normally and underdeveloped shoots from shaded and well-exposed canopies. Positive effects of canopy management practices were mainly noticeable regarding the acid content. Higher titratable acidity and tartaric acid levels and lower pH were measured in these canopies. No difference in the malic acid content was found between shaded and well-exposed canopies, resulting in a higher tartaric:malic acid ratio for the latter. No statistically significant differences in grape composition and quality were found between the normally and underdeveloped shoots at five weeks after véraison. It was assumed that the assimilates needed for berry ripening in the underdeveloped shoots originated in other organs than the leaves, such as adjacent shoots and the rest of the permanent structure of the vine (cordon, trunk, roots). The lower levels of starch that accumulated in underdeveloped shoots supported this deduction. Short shoots probably decreased the grape quality of adjacent normal shoots and affected reserve accumulation and shoot ripening negatively. Despite grape composition differences not being significant for all measured parameters, the results clearly indicated that shoot heterogeneity in grapevine canopies should be avoided.

2. INTRODUCTION

Due to the ever-increasing national and international market competition and requirements, wine industries must be committed to produce grapes and must of excellent quality (Hunter & Archer, 2001). Increased grape quality must thus be obtained without a decrease in the yield or longevity of the vine. Therefore, carbon allocation to the clusters must be optimised (Hunter, 2000) without detrimentally affecting growth and development in other parts of the vine.

Photosynthesis is particularly important in relation to the total yield and the distribution of assimilates to the different plant parts (Calò *et al.*, 1995) – thus improved radiation should result in increased yield and quality. This was confirmed by Rojas-Lara & Morrison (1989) who found delayed berry growth and ripening in shaded canopies, while optimal ripening also seemed to be inhibited (Archer, 1988). Smart *et al.* (1989) stated that shaded canopy microclimates were unfavourable to wine quality, while Jackson & Lombard (1993) linked shading with unbalanced must that resulted in poor wine quality. Keller & Hrazdina (1996) stressed the importance of the microclimate for obtaining optimum quality grapes by stating that fruit quality is primarily determined by light intensity during véraison. Except for the increased photosynthetic activity of the leaves, light inside vine canopies also affected grape composition directly, since Valenti *et al.* (1995) linked berry composition with the quantity of light reaching each cluster during ripening. Reynolds *et al.* (1986) also found that increased cluster exposure improved the composition.

According to Hunter (1991) grape yield and composition were negatively affected by too vigorous growth. The latter indicates unbalanced vines where assimilates are mostly translocated to the vegetative parts of the vine, while the clusters are neglected. The consequences may be increased shoot growth and leaf area, as well as too many secondary shoots, water shoots and the outburst of basal buds. The higher the leaf area density, the higher the interior canopy shade (Smart *et al.*, 1985a) and the lower the PPFD (Dokoozlian & Kliewer, 1995), with the already discussed detrimental effects on grape quality. High vegetative growth is also counterproductive to grape production and quality due to the strong competition by the growing shoot tips for newly produced carbohydrates (Boulton *et al.*, 1998).

According to Scienza *et al.* (1995) the balances between yield and vegetative growth are useful to explain variation in wine quality. High vegetative:reproductive growth in the grapevine can be seen as under-cropping where the rate at which assimilates are utilised and stored is less than that at which it is supplied to the vine tissues (Baysdorfer & Bassham, 1985, according to Iacono *et al.*, 1995). This usually results in excessive vegetative growth and delayed maturation (Bravdo & Naor, 1995). Over-cropping, on the other hand, is when there is a high reproductive to vegetative growth ratio (Bravdo & Naor, 1995) where the capacity of assimilate provision is insufficient for the demand of

the sink tissues (Iacono *et al.*, 1995). This will result in delayed maturation, poor colouration and low aroma and flavour (Bravdo & Naor, 1995).

This ratio could also be applied to individual shoots where underdeveloped shoots could be seen as over-cropped with insufficient leaf area to adequately ripen their clusters (Peterson & Smart, 1975). This could be why short shoots imported more assimilate from adjacent shoots than did normally developed shoots (Koblet, 1977). The assumption could thus be made that the presence of underdeveloped shoots in the canopy could be responsible for a decrease in the grape quality of the other, stronger shoots from the same vine and in fact the total yield.

Grape composition in a vineyard is usually described as a mean value (Trought, 1996), although the variation around the mean may have an important impact on quality. Even among clusters on the same vine and among berries within a cluster, there were always a degree of variability in berry composition and stage of development (Rojas-Lara & Morrison, 1989). When the variation around the mean was large, the potential for the presence of overripe and unripe flavours in the must and wine was increased, even though the average composition seemed acceptable (Trought, 1996). Different shoot lengths in a vine would thus impair the overall quality (Archer, 2001), as well as increasing the variation in composition of the yield. Equality in shoot growth thus seems important for the production of homogeneous, top quality grapes.

The grape berry is non-climacteric with a double sigmoid growth curve (Hunter, 1991). The first growth phase takes the berries to the hard, green, slow growing phase, while berry ripening processes occur during the second cycle that begins at véraison (Coombe, 1992a). The grape ripening stage is normally associated with cell enlargement, softening, colouring and sweetening, with a decrease in acidity and astringency, loss in chlorophyll and an increase in aroma (Hunter, 1991).

The accumulation of sugars, which was mainly stored in the form of hexoses in the flesh (Ollat & Gaudillère, 1997), was favoured at véraison (Hunter & Visser, 1988). After a considerable initial increase in sugar concentration, the curve tended towards a plateau (Coombe, 1992b). Dense canopies had a negative effect on sugar concentration in the clusters (Smart *et al.*, 1985b; Coombe, 1987b; Archer, 1988; Jackson & Lombard, 1993; Iacono *et al.*, 1995; Kliewer &

Dokoozlian, 2000; Tomasi *et al.*, 2000; Bergqvist *et al.*, 2001), associated with a decrease in juice glucose and fructose concentrations, as well as the glucose:fructose ratio (Smart *et al.*, 1988).

According to Hunter *et al.* (1991a) and Hunter & Ruffner (2001) the highest total malic and tartaric acid concentration was reached at pea berry size. It was found that the malic acid decreased from véraison to ripeness (Iland & Coombe, 1988; Hunter, 1991; Hunter *et al.*, 1991a; Coombe, 1992b; Terrier *et al.,* 1997) due to malic acid metabolism during ripening (Iland & Coombe, 1988). The tartaric acid content of grape berries, however, changed very little from véraison to full ripeness (Iland & Coombe, 1988; Hunter *et al.*, 1991a; Coombe, 1992b; Gutiérrez-Granda & Morrison, 1992). An increase in the degree of shading in the canopy was associated with an increase in the juice malic acid content (Coombe, 1987b; Kliewer & Bledsoe, 1987; Archer, 1988; Smart *et al.*, 1988; Archer & Strauss, 1989; Kliewer & Dokoozlian, 2000) and a decrease in the tartaric acid content (Smart *et al.*, 1985b; Archer, 1988; Archer & Strauss, 1989). The effect of shading on the total acidity seemed to depend on the tartaric:malic acid ratio, since both higher and lower total acid content of berries has been found by different sources. The occurence of higher concentrations of organic acids in shade was explained by the lower rate of malic acid metabolism and thus higher malic acid levels (Archer & Strauss, 1989). When lower titratable acid was found (Smart *et al.*, 1985b), it was probably due to a lower tartaric acid content (Archer, 1988).

As expected, an increase in pH after véraison was found with ripening (Iland & Coombe, 1988; Hunter, 1991; Gutiérrez-Granda & Morrison, 1992), while a negative correlation between the average light values in the canopy and the pH was generally found (Smart *et al.*, 1985b; Kliewer & Bledsoe, 1987; Archer, 1988; Archer & Strauss, 1989; Kliewer & Dokoozlian, 2000; Bergqvist *et al.*, 2001).

The increased potassium content in all the berry tissues after véraison with ripening (Conradie, 1981; Coombe, 1987a; Iland & Coombe, 1988; Coombe, 1992b; Gutiérrez-Granda & Morrison, 1992) also affected the pH, since it forms insoluble salts with tartaric acid that more often leads to an increase in pH (Hunter, 1991). Kliewer & Bledsoe (1987) found a negative correlation between the average light values and potassium, while potassium was also found to increase in unbalanced and vigorous vines with an increase in the level of

shading (Archer, 1988; Archer & Strauss, 1989; Hunter, 1991; Kliewer & Dokoozlian, 2000).

The highest anthocyanin content in the berries was found 20 to 30 days after véraison (Hunter *et al.,* 1991b), since the accumulation of precursors for anthocyanin synthesis was favoured at véraison (Hunter & Visser, 1988). During the later ripening stages a decline in the total anthocyanin content of berries was noted (Hunter *et al.*, 1991b; Haselgrove *et al.,* 2000). The berry skin colour was related to at least three factors operating separately (Iacono *et al.*, 1994), namely berry sugar, cluster exposure and crop load (leaf area/fruit mass ratio). A study done by Hunter *et al.* (1991b) showed a close positive correlation between sugar levels in the berry skins and the anthocyanin concentration. It was generally found that light exposure led to higher anthocyanin concentrations than shaded conditions (Archer, 1988; Smart *et al.*, 1988; Calò *et al.*, 1995; Keller & Hrazdina, 1996; Haselgrove *et al.*, 2000; Kliewer & Dokoozlian, 2000; Tomasi *et al.*, 2000; Bergqvist *et al.*, 2001). Coombe (1987b) and Bergqvist *et al.* (2001) found an increase in anthocyanins with an increase in temperature, but only up to a certain point, whereafter a decrease in anthocyanins with a further increase in temperature occurred. A decrease in both the total anthocyanins and the colour density was found in unbalanced and too vigorous vines (Hunter, 1991).

Calò *et al.* (1995) reported that the precursors of aroma components were synthesized in the leaves, while the synthesis of the components themselves occurred in the grape berries. Aroma components were mainly accumulated in the berry skin (Bravdo & Naor, 1995; Calò *et al.*, 1995). Although the total phenol concentration decreased steadily after an increase during the early ripening process (Kataoka *et al.*, 1983), it was found by Singleton (1966) that the total phenols per berry increased until rather late in the maturation stage, which indicated a continuous synthesis of phenolic compounds. According to Archer (1981), Winkler *et al.* (1974) stated that the accumulation of flavour components occurred during the later ripening stages of most grape cultivars.

The region where the grapes are cultivated plays an important role in determining the flavour compounds found in the berries. According to Marais (1992) higher carotenoid levels were found in grapes produced in hotter areas than in those produced in cooler regions. A greater possibility existed for the development of undesired, unripe, herbaceous characters in the berries as the level of shading in the canopy increased (Haselgrove *et al.*, 2000). Lower phenol content was also

found under vigorous growth conditions where the canopy had a shaded interior (Smart *et al.*, 1985b; Coombe, 1987b; Smart *et al.*, 1988; Hunter, 1991). Sunlight exposure of the clusters increased the levels of phenolic compounds, monoterpenes (Hunter & Fouché, 2000; Kliewer & Dokoozlian, 2000) and quercitin and decreased the methoxypyrazine (Kliewer & Dokoozlian, 2000) and carotenoid levels (Marais, 1992). It is thus important for the canopy to be well exposed before véraison to enhance the accumulation of various flavour compounds. This could be obtained by the correct canopy management practices where the better sunlight exposure changed the flavour profile and enhanced the typical flavour of the cultivar (Volschenk & Hunter, 2001) and resulted in wines with more complexity (Hunter & Fouché, 2000).

In this study, certain berry ripening and quality parameters were monitored for five weeks after véraison in an attempt to quantify any differences that may exist in the berry composition, quality or ripening dynamics of normally and underdeveloped shoots under well-exposed and shaded conditions.

3. MATERIALS AND METHODS

Experimental vineyard

A seven year old *Vitis vinifera* L. cv. Shiraz, clone SH1A, grafted onto Richter 99 (*Vitis Berlandieri* x *Vitis rupestris*), clone RY2A, vineyard was used for this study. The vineyard is situated at the experimental farm of the Agricultural Research Council (ARC) Infruitec-Nietvoorbij near Stellenbosch in the Western Cape. The vines are spaced 2.75 × 1.5 m on a Glenrosa soil with a western aspect (26° slope) and trained onto a 7-wire lengthened Perold trellising system with movable canopy wires (VSP). Rows were orientated in a North-South direction.

Micro sprinkler irrigation was applied at pea size berry and at véraison. Pest and disease control was applied during the growth season according to the standard program of the ARC.

Experiment design

The experiment was laid out as a completely randomised 2×4×2 factorial design. The three factors were: degree of canopy exposure (well-exposed and shaded canopies); ripening stages (one, three, four and five weeks after véraison); and

level of shoot development (normally and underdeveloped shoots). There were three replications for each of the 16 treatment combinations.

Shaded canopies were only shoot positioned and topped, whereas additional suckering and leaf thinning were applied to create well-exposed canopies. Selection of underdeveloped shoots was based on length and comparative lack of lignification at véraison (Fig.1, Chapter 3).

Measurements

All the clusters on the shoots sampled were used. The shoots were randomly selected as described in Chapter 3.

Determination of sugars and acids: Sugars (glucose and sucrose) and organic acids (malic and tartaric acid) were extracted and analysed by gas liquid chromatography (GLC) after silylation, as described by Hunter & Ruffner (2001). Five grams of fresh berries (representative sample, including the skin, flesh and pips) were homogenised in 50 mL of 50% (v/v) methanol by means of a Janke & Kunkel Ultra-Turrax T25 macerator for 3 min. at 20 500 rpm. The bottle was capped and kept in boiling water for 10 min. After centrifugation for 15 min. at 16 318 g, the supernatant was removed and stored. The pellet was resuspended in another 50 mL of 50% (v/v) methanol, the maceration repeated for 2 min. and centrifugation completed as before. The pellet was then discarded. The supernatants were combined and neutralised (pH 7.0) with 1 M NaOH. As internal standard, D(-)salycin was added at a concentration of 0.5 mg/mL and the extract concentrated to approximately 5 mL in a rotary evaporator at 40°C under vacuum. The concentrate was then transferred quantitavely to a measuring cylinder and the evaporator flask washed with several portions of water to a total of 20 mL. This was well mixed and a 1 mL aliquot removed to an Eppendorf tube, frozen, and lyophilised. After lyophilisation, samples were silylated by dissolving in 0.7 mL pyridine (kept over NaOH pellets) and addition of 200 μL HMDS (1,1,1,3,3,3-hexamethyl-disilazane) and 100 μL TMCS (trimethylchlorosilane), with vortexing in between. Samples were then heated to 60°C in an oven for 24 h, vortexed, and stored in a desiccator. The clear supernatant (2 μL) was injected into the GC. For calibration purposes, a standard mixture of sugars and organic acids was brought to dryness in the rotary evaporator, dissolved in 1.5 mL water, frozen, lyophilised, and silylated as above.

The GLC (Varian Vista 6 000) conditions were as follows: A 25 m Supelco SE-54 capillary column with 0.2 mm i.d. was used. The injection and detector (FID) temperatures were 200°C and 260°C, respectively. The column limit was set to 280°C. The temperature program comprised an initial temperature of 160°C, held for 0.5 min.; 160-200°C at a rate of 5.0°C/min.; 200-260°C at 20°C/min., held for 15 min. Analysis time was 26.5 min. Helium gas served as carrier gas.

Soluble solids (°B), pH and total titratable acidity were determined using standard laboratory methods.

Determination of colour and phenolics: [Described in Hunter *et al.* (1991b).] A random sample of 100 berries was stored at –20°C until required for analyses. Skins were separated from pulps by gentle squeezing between thumb and forefinger. Any pulp adhering to skins was removed. Skins were then rinsed in distilled water, blotted dry, and the fresh mass determined. Skins were frozen at –20°C just prior to freeze-drying with a Chriss Alpha freeze-drying unit. Dried skins were weighed, ground in a Sorvall Omni-mixer, and stored at room temperature until used.

One gram of freeze-dried skin material was extracted in 30 mL methanolic 0.1% HCl solution (pH 3.5) at room temperature using a Janke & Kunkel horizontal shaker (model HS 500) operating at 250 rpm for 15 minutes. After centrifugation at 27 138 g for 15 minutes, the supernatant was decanted and the process repeated twice. Supernatants were combined and acidified to pH 1.0 using 1 M HCl. The solution was then made up to 100 mL with extraction solvent (pH 1.0) and left in the dark at room temperature for approximately one hour. After proper dilution (1:4), absorbancies of anthocyanins (420 nm and 520 nm) and total phenolics (280 nm) were determined with a LKB Biochrom Utrospec spectrophotometer (II E) using 2 mm quartz cells.

Statistical analyses

Due to the nature of the data, a non-parametric bootstrap analysis was used when it proved to be more practical than factorial ANOVA. The significance of the results was evaluated using 95% confidence intervals. Since only three replications per treatment were used, tendencies, rather than absolute statistical significances, were discussed. During interpretation of the figures, differences were considered significant when no overlapping of the 95% confidence intervals occurred.

4. RESULTS

Sugars: During the five weeks after véraison the °Balling of all the berries increased. No significant difference in berry soluble solids was found between normally and underdeveloped shoots in both the shaded and well-exposed canopies. The degree of canopy exposure also did not seem to affect the °Balling (Fig. 1).

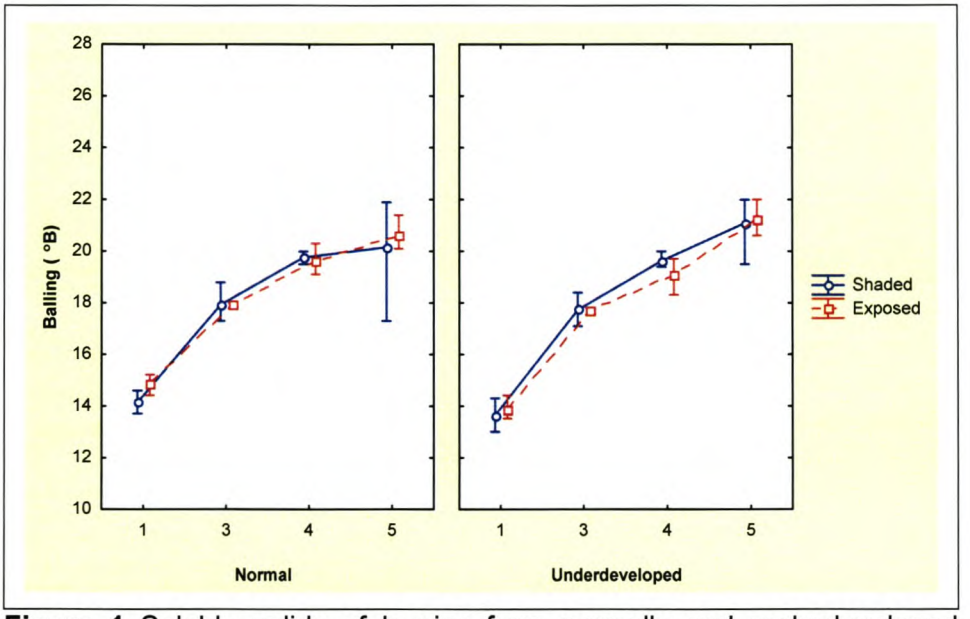

Figure 1 Soluble solids of berries from normally and underdeveloped shoots in shaded and well-exposed canopies at one, three, four and five weeks after véraison. Error bars indicate 95% confidence intervals (bootstrap analysis).

When the levels of specific sugars were determined five weeks after véraison, no significant differences in the glucose or sucrose content of the berries from normally and underdeveloped shoots in shaded or exposed canopies were found (Figs. 2 & 3).

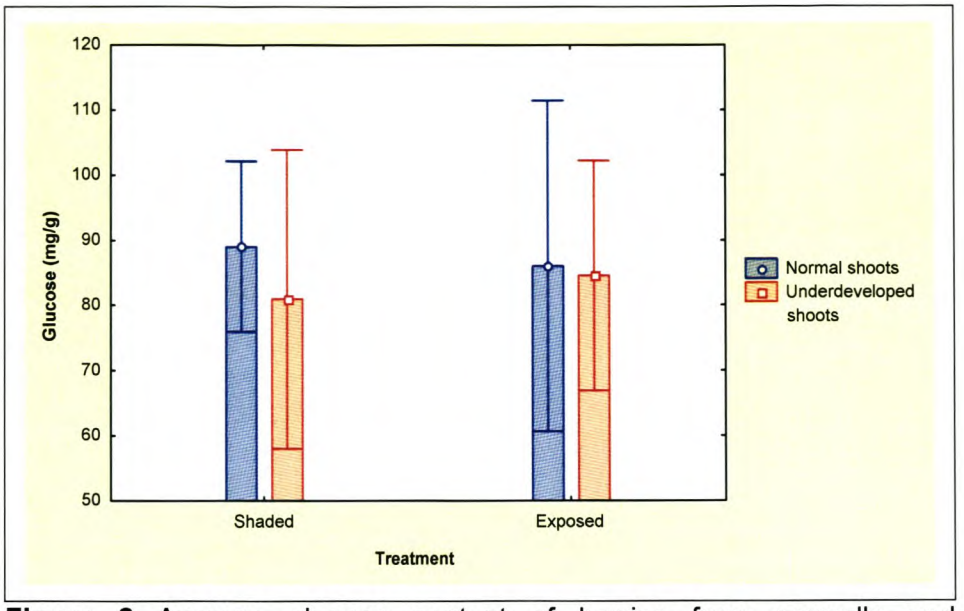

Figure 2 Average glucose content of berries from normally and underdeveloped shoots in shaded and well-exposed canopies at five weeks after véraison. Error bars indicate 95% confidence intervals.

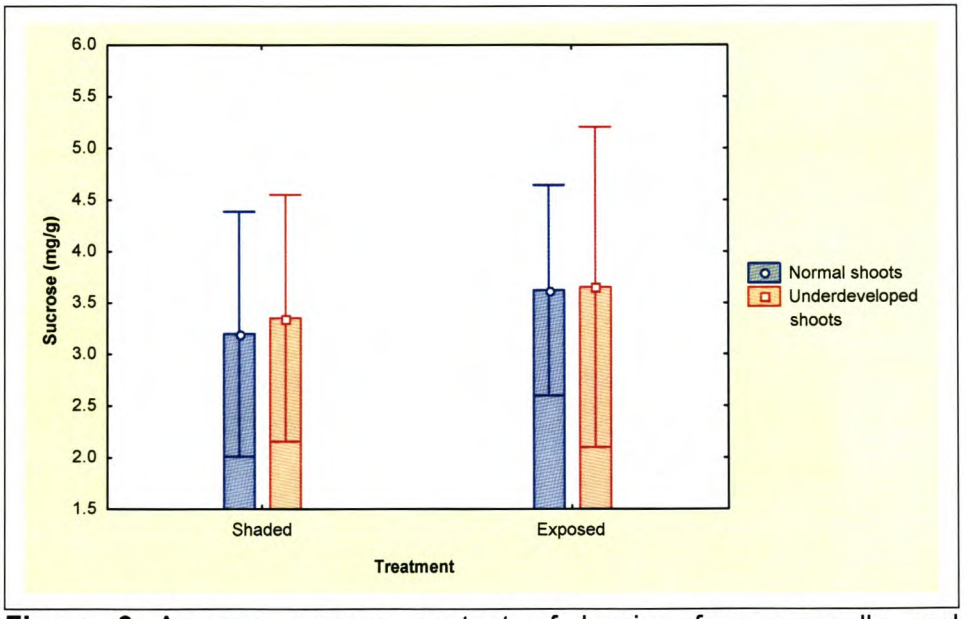

Figure 3 Average sucrose content of berries from normally and underdeveloped shoots in shaded and well-exposed canopies at five weeks after véraison. Error bars indicate 95% confidence intervals.

Acids and pH: The titratable acidity in all the berries decreased with ripening (Figs. 4 & 5). It seemed as if higher average acid levels occurred in the berries of the underdeveloped compared to the normal shoots (Fig. 4). The degree of canopy exposure appeared to affect the acid levels, since higher titratable acidity

was found in the berries from exposed versus shaded canopies. This difference between the canopies was found to be statistically significant for the normally developed shoots five weeks after véraison (Fig. 5).

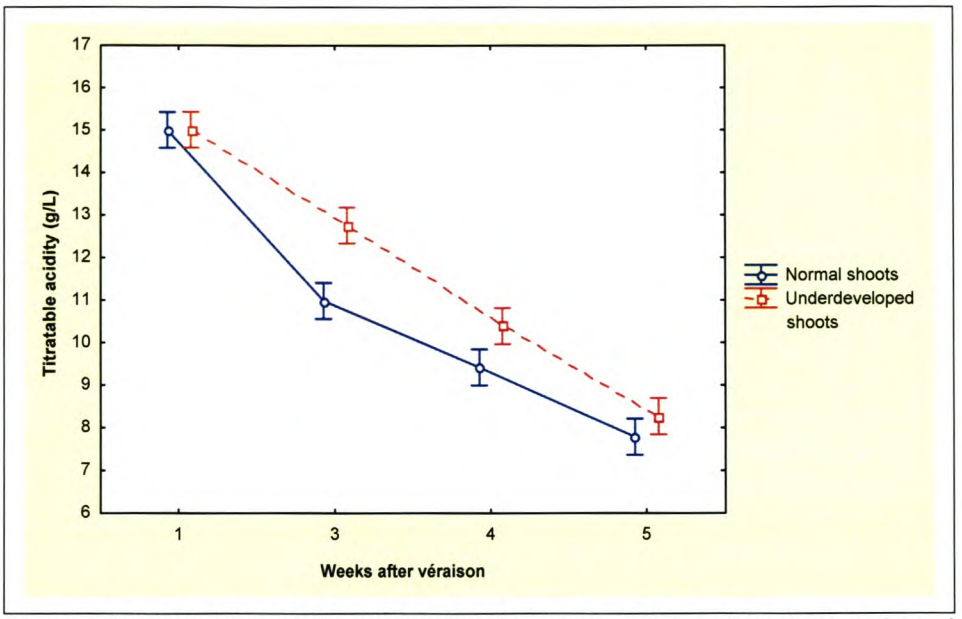

Figure 4 Titratable acidity of berries from normally and underdeveloped shoots at one, three, four and five weeks after véraison. Error bars indicate 95% confidence intervals.

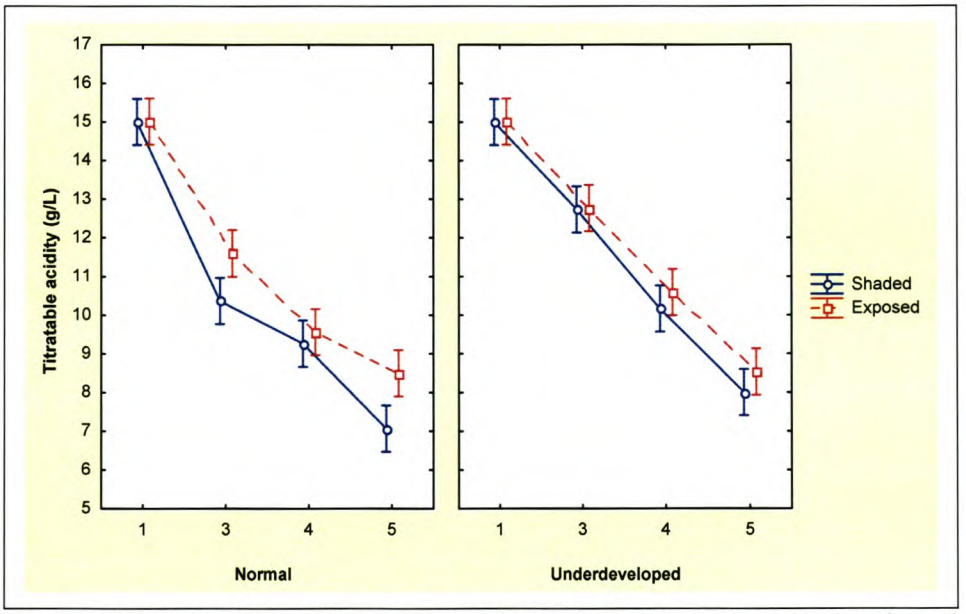

Figure 5 Titratable acidity of berries from normally and underdeveloped shoots in shaded and well-exposed canopies at one, three, four and five weeks after véraison. Error bars indicate 95% confidence intervals.

When individual acids were measured five weeks after véraison, no statistically significant differences were found between the malic ($p \leq 0.13$) and tartaric acid ($p \leq 0.55$) contents of normally and underdeveloped shoots in either shaded or well-exposed canopies (Figs. 6 & 7). However, the malic acid concentrations seemed lower and the tartaric acid concentrations higher in the berries of normal shoots. Less variation is again noticeable in the values obtained for normal shoots. Canopy exposure seemed to affect the tartaric acid content to a small degree, since little higher average tartaric acid levels were found for the exposed canopies ($p \leq 0.06$) (Fig. 7).

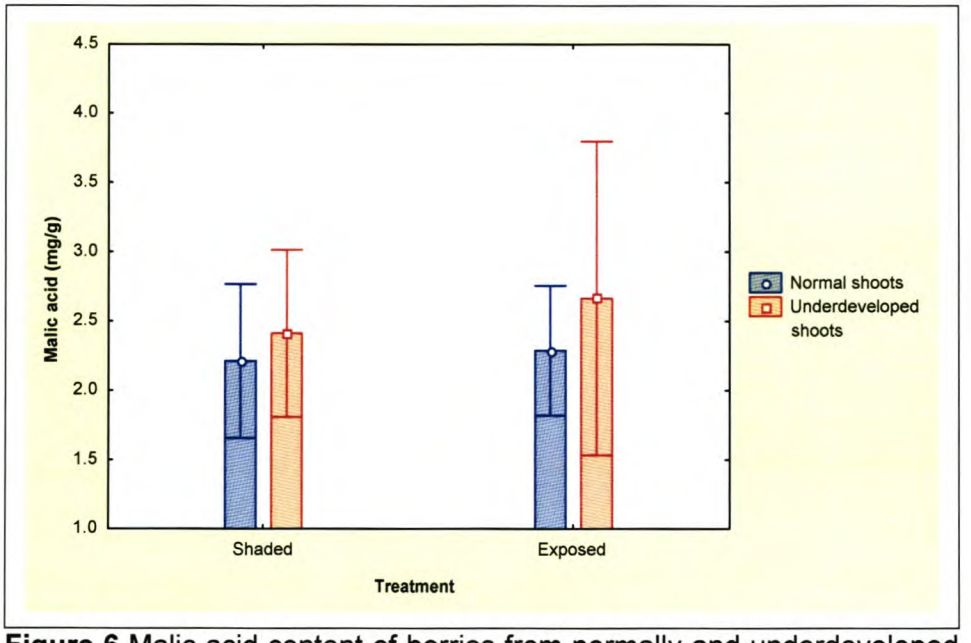

Figure 6 Malic acid content of berries from normally and underdeveloped shoots in shaded and well-exposed canopies at five weeks after véraison. Error bars indicate 95% confidence intervals.

The acid composition of the berries from the normal shoots was possibly more conducive to quality wine making than that from the underdeveloped shoots, since the average tartaric:malic acid ratio seemed higher in the former (Fig. 8).

In concurrence with the acid data, the pH of all the berries increased with ripening (Figs. 9 & 10). Lower pH levels was found for the berries from the exposed than shaded canopies, while it seemed as if lower pH levels were constantly measured from berries of underdeveloped compared to normally developed shoots.

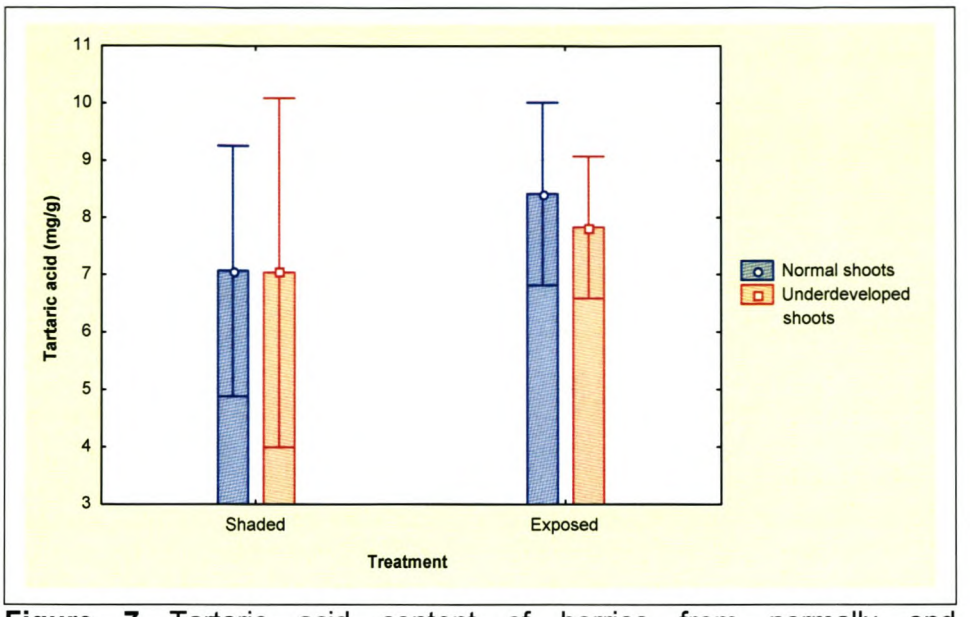

Figure 7 Tartaric acid content of berries from normally and underdeveloped shoots in shaded and well-exposed canopies at five weeks after véraison. Error bars indicate 95% confidence intervals.

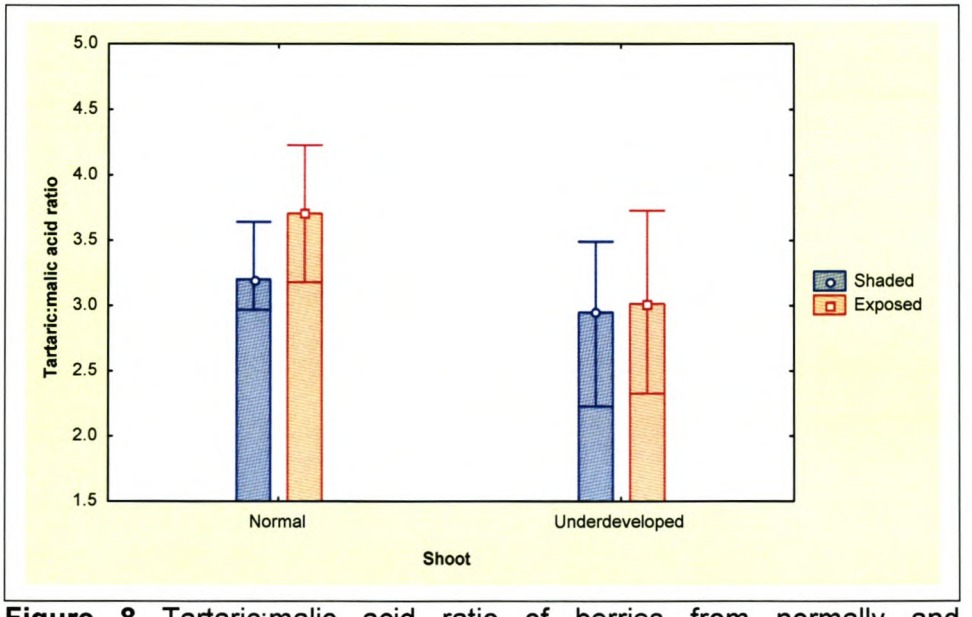

Figure 8 Tartaric:malic acid ratio of berries from normally and underdeveloped shoots in shaded and well-exposed canopies at five weeks after véraison. Error bars indicate 95% confidence intervals (bootstrap analysis).

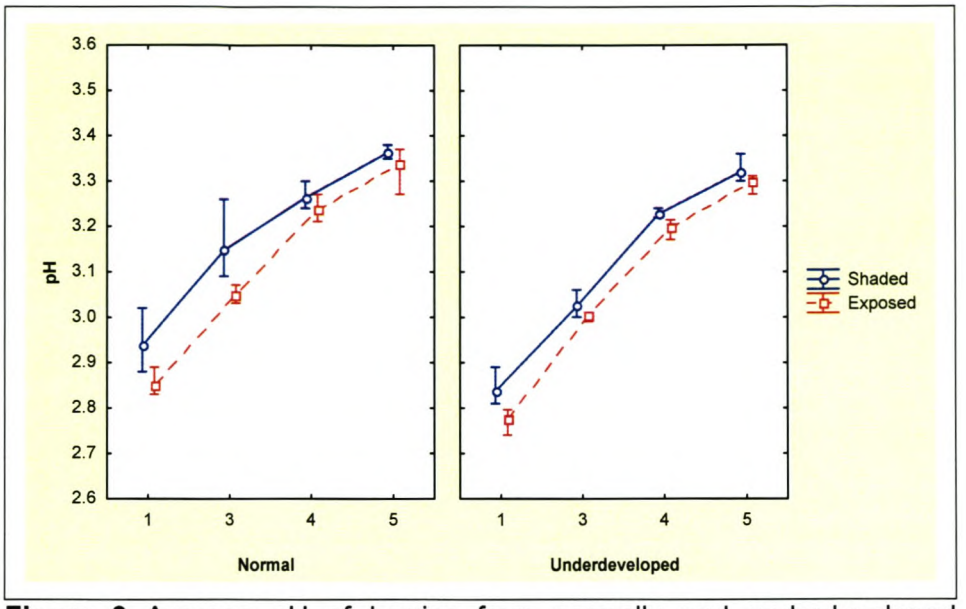

Figure 9 Average pH of berries from normally and underdeveloped shoots in shaded and well-exposed canopies at one, three, four and five weeks after véraison. Error bars indicate 95% confidence intervals (bootstrap analysis).

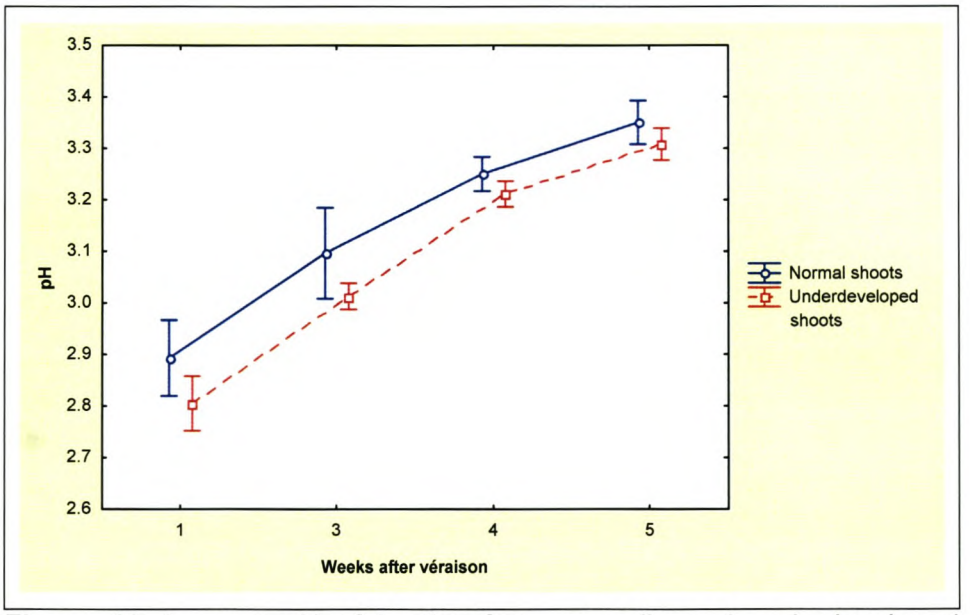

Figure 10 Average pH of berries from normally and underdeveloped shoots at one, three, four and five weeks after véraison. Error bars indicate 95% confidence intervals.

Phenols: The development of phenols in the berries from normal shoots in the shaded canopies appeared to have been more irregular than in the exposed canopies. Just after véraison, significantly higher phenol levels were found in berries from well-exposed than from shaded canopies, but the phenols in the latter canopies increased rather significantly between the first and third week after véraison. No significant difference in the phenol content of berries of normal shoots was found between shaded and well-exposed canopies (Fig. 11).

The berry phenol content of underdeveloped shoots increased regularly during the five weeks after véraison, with no significant differences found at any time between the shaded and well-exposed canopies (Fig. 11).

No statistically significant difference between the phenol content of the normal and underdeveloped shoots was found during ripening (Fig. 11).

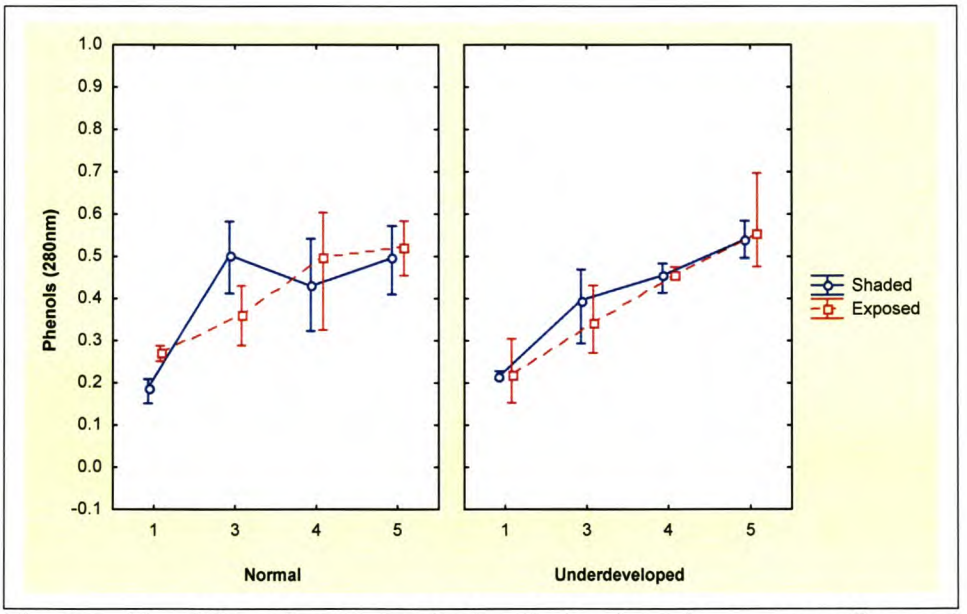

Figure 11 Skin phenol content of berries from normally and underdeveloped shoots in shaded and well-exposed canopies at one, three, four and five weeks after véraison. Error bars indicate 95% confidence intervals (bootstrap analysis).

Skin colour: There seemed to have existed certain differences in the skin colour intensity and density curves of normally and underdeveloped shoots over the five weeks after véraison (Figs. 12 & 13).

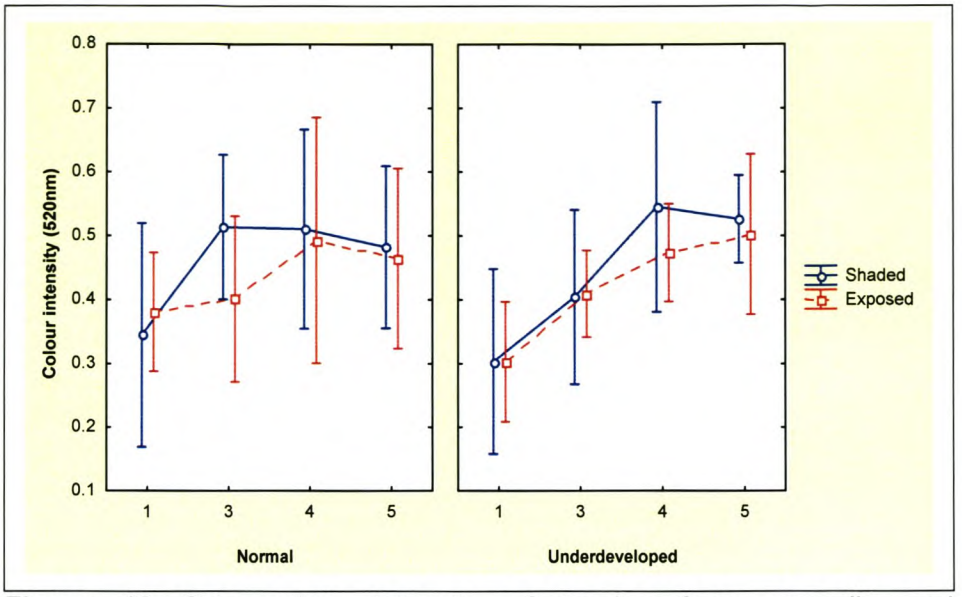

Figure 12 Skin colour intensity of berries from normally and underdeveloped shoots in shaded and well-exposed canopies at one, three, four and five weeks after véraison. Error bars indicate 95% confidence intervals.

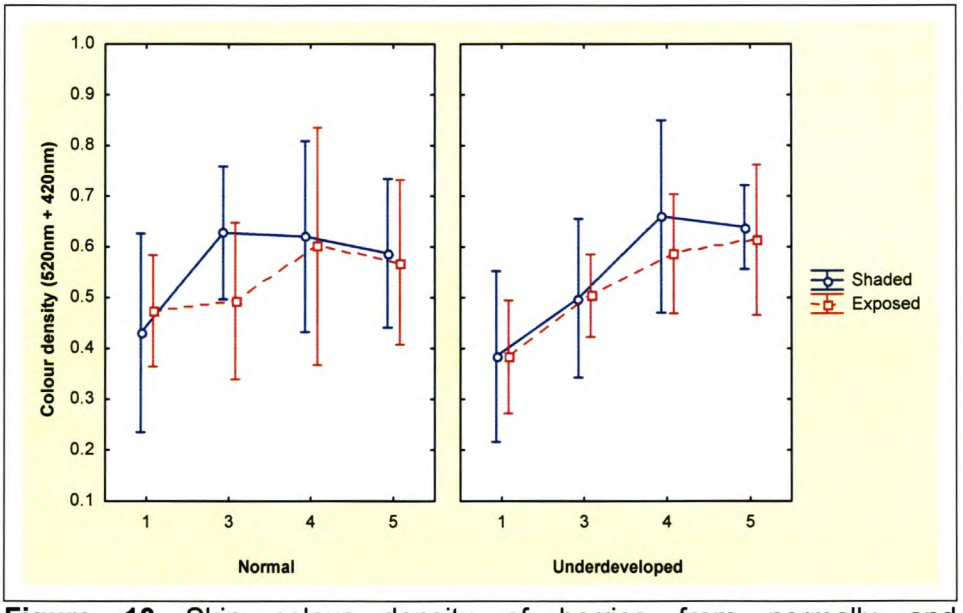

Figure 13 Skin colour density of berries from normally and underdeveloped shoots in shaded and well-exposed canopies at one, three, four and five weeks after véraison. Error bars indicate 95% confidence intervals.

The measurements of the berries from the normal shoots in the shaded canopies appeared to have reached a maximum at three weeks after véraison, whereafter it slightly decreased. In the exposed canopies the most apparent colour increase for the normal shoots occurred at four weeks after véraison, whereafter it also decreased slightly (Figs. 12 & 13).

Regarding the underdeveloped shoots, the colour measurements of the berries in the shaded canopies also seemed to have reached a maximum before those in the exposed canopies at four weeks after véraison, whereas berry colour in the exposed canopies appeared to have increased a little in the fifth week after véraison. As in the case of the normal shoots, no significant effect of canopy exposure was found on the colour intensity and density of berry skins from underdeveloped shoots at five weeks after véraison (Figs. 12 & 13), although it seemed as if the average levels were constantly a little lower in the exposed canopies during the earlier stages of berry ripening (Fig. 14).

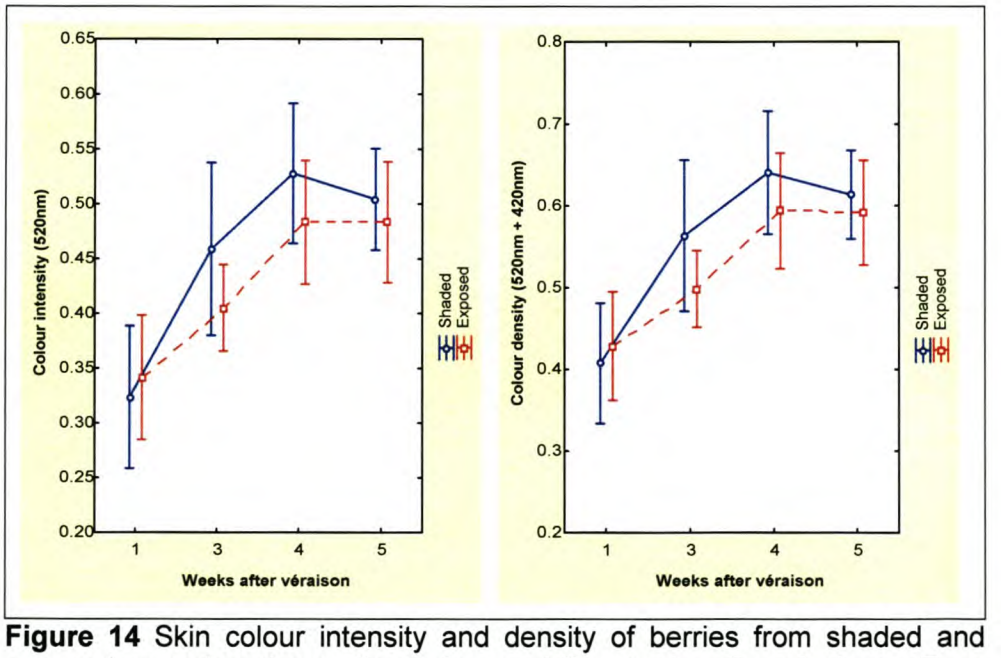

Figure 14 Skin colour intensity and density of berries from shaded and exposed canopies at one, three, four and five weeks after véraison. Error bars indicate 95% confidence intervals.

During the first three to four weeks after véraison, it seemed as if the average skin colour of the normal shoots were higher than that of the underdeveloped shoots, but the order appeared to have reversed at five weeks after véraison.

Still, no statistical significant difference in the skin colour intensity or density was found between normally and underdeveloped shoots at any time after véraison (Figs. 15 & 16).

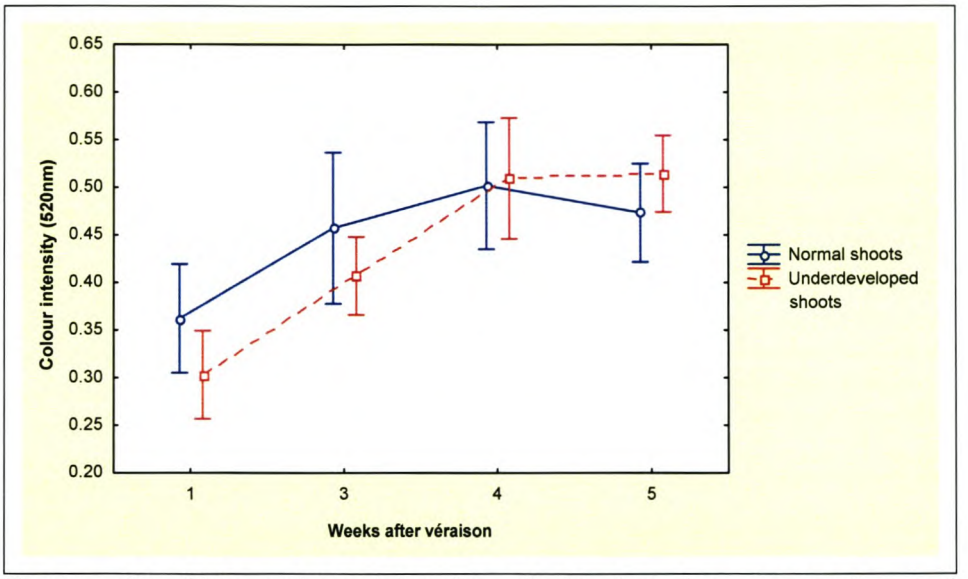

Figure 15 Skin colour intensity of berries from normally and underdeveloped shoots at one, three, four and five weeks after véraison. Error bars indicate 95% confidence intervals.

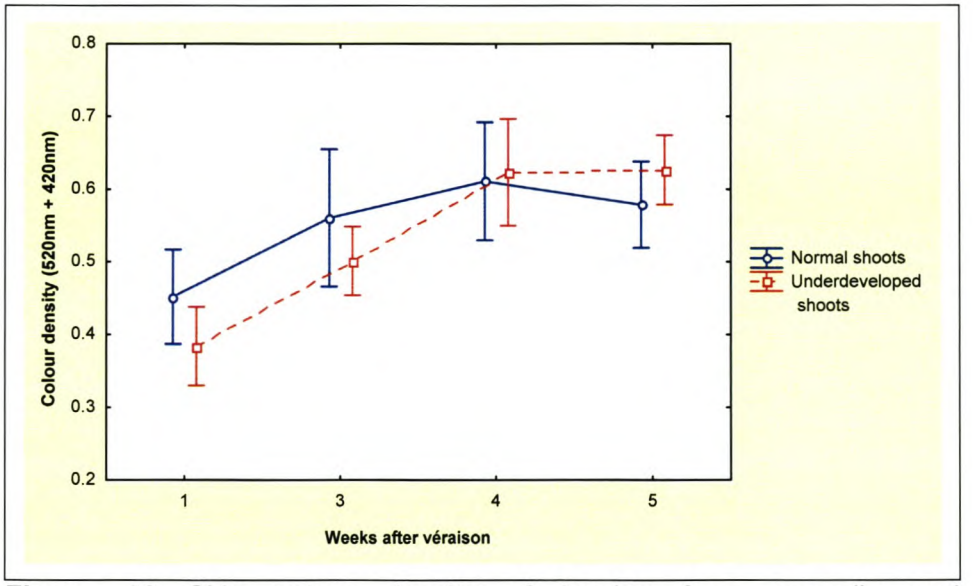

Figure 16 Skin colour density of berries from normally and underdeveloped shoots at one, three, four and five weeks after véraison. Error bars indicate 95% confidence intervals.

It is noticeable that ripening seemed to proceed at a more gradual rate in normal shoots and under exposed conditions. This also seemed to be the case for grape development as discussed in the previous chapter. This is very important as it allows more possibilities in terms of harvesting date and harvesting for different wine styles.

5. DISCUSSION

Wine quality is primarily dependent on the quality of the grapes used. Since many cellar decisions are based on the expected quality of wine that is going to be produced, it is important for the winemaker and viticulturist to have certain parameters for determining the grape, and ultimate wine, quality. Therefore, knowledge of how the levels of different grape components change with berry ripening is of the utmost importance.

Sugars: It was found that the sugar concentration increased similarly to the pattern described by Coombe (1992b) who stated that after a considerable initial increase in sugar concentration, the curve tended towards a plateau. Although, according to literature, delayed berry ripening (Rojas-Lara & Morrison, 1989) and thus lower sugar concentrations were found in shaded canopies (Smart *et al.*, 1985b; Coombe, 1987b; Archer, 1988; Jackson & Lombard, 1993; Iacono *et al.*, 1995; Kliewer & Dokoozlian, 2000; Tomasi *et al.*, 2000; Bergqvist *et al.*, 2001), the different degrees of canopy exposure did not affect the sugar concentration of the berries in this case.

Despite the sub-optimal total leaf area per gram grape berries calculated for underdeveloped shoots (Chapter 6) as well as the lower photosynthetic activity from three weeks after véraison (Chapter 4), no statistically significant difference in the sugar concentration between the berries from the normally and underdeveloped shoots was found. It further seemed as if the sugar content of all the berries at five weeks after véraison comprised of the same components in comparable amounts, since no significant difference in the glucose and fructose concentrations of berries from normally and underdeveloped shoots in both shaded and exposed canopies was found.

Berry sugar concentration is considered one of the most, if not the most, important criterion for grape quality in cooler vine growing areas, since difficulty is

often experienced in obtaining the required sugar levels due to the low temperatures and little sunlight. In warmer areas, such as South Africa, other components such as acids, colour and phenol content should also be considered for determining grape quality (Archer, 1981).

Acids and pH: A decrease in the titratable acidity was found with ripening. This was probably due to malic acid metabolism during ripening (Iland & Coombe, 1988), since the tartaric acid content of grape berries is known to remain relatively constant between véraison and ripeness (Iland & Coombe, 1988; Hunter *et al.*, 1991a; Coombe, 1992b; Gutiérrez-Granda & Morrison, 1992). The malic and tartaric acid levels were only determined at five weeks after véraison, therefore no statements regarding the period prior to that can be made.

It seemed as if higher berry acid content was associated with exposed canopies, since non-significantly higher average values were constantly measured in these canopies, including in the fifth week after véraison. This could have been due to the higher levels of tartaric acid found in the berries from the well-exposed compared to those in shaded canopies at five weeks after véraison, although the difference was not significant. It is quite possible that higher tartaric acid contents were also responsible for the higher acid levels in the exposed canopies during the previous weeks, since lower total acidity in berries from shaded canopies was ascribed to lower tartaric acid content (Archer, 1988).

Higher titratable acidity levels were continuously found in berries from underdeveloped compared to normally developed shoots after véraison. At five weeks this difference was not statistically significant and could possibly be explained by the non-significant higher malic acid content found in the berries of the underdeveloped shoots. It should, however, be kept in mind that the total titratable acidity also includes other acids than tartaric and malic acid, such as citric and succinic acid that could affect the must balance and wine quality.

Although it could be possible that the acid composition of the berries from the normally developed shoots was more conducive to quality wine making than that from the underdeveloped shoots, the tartaric:malic acid ratio was not significantly higher.

An increase in the pH during ripening was found, which is in accordance with Iland & Coombe (1988), Hunter (1991) and Gutiérrez-Granda & Morrison (1992).

Lower pH levels were continuously measured for the berries from the underdeveloped shoots and exposed canopies, which reflected their higher titratable acidity than berries from normal shoots and shaded canopies. Lower pH levels in exposed canopies has also been reported by Smart *et al.* (1985b), Kliewer & Bledsoe (1987), Archer (1988), Archer & Strauss (1989), Kliewer & Dokoozlian (2000) and Bergqvist *et al.* (2001).

Therefore, based on the sugar and acid analysis, no significant difference in the berry composition of normally and underdeveloped shoots was found at five weeks after véraison.

Phenols: Although the concentration levels of aroma compounds are not comparable to sugars or acids, the phenol content of must can be crucial to quality by affecting the colour, astringency, tannin character and ageing potential of red wine (Hunter, 1991). According to Bravdo & Naor (1995) and Calò *et al.* (1995) most of the phenolic compounds accumulated in the berry skin, in constrast with Boulton *et al.* (1998) who found only 30 percent of the total phenol content in the skins.

The level of shade in the canopy and the degree of cluster exposure affected the total phenol content as well as composition in the berries. Lower phenol content was found under vigorous growth conditions where the canopy had a shaded interior (Smart *et al.*, 1985b; Coombe, 1987b; Smart *et al.*, 1988; Hunter, 1991), while sunlight exposure of the clusters increased the levels of phenolic compounds, monoterpenes (Hunter & Fouché, 2000; Kliewer & Dokoozlian, 2000) and quercitin and decreased the methoxypyrazine (Kliewer & Dokoozlian, 2000) and carotenoid levels (Marais, 1992). However, no significant difference in the total phenol concentration between the shaded and exposed canopies was found for the normally or underdeveloped shoots at five weeks after véraison.

The degree of canopy exposure did seem to affect the time and pattern of phenol accumulation in the berries of normal shoots. It appeared as if the accumulation in the shaded canopies occurred later during the ripening stage than in the exposed canopies. This led to the assumption that either phenol accumulation was delayed in the shaded canopies, or the phenol profile of the berries differed between the canopies. However, since no specific phenols were analysed, the latter assumption was based on the literature. It was found that the better sunlight exposure due to canopy management changed the flavour profile and

enhanced the typical flavour of the cultivar (Volschenk & Hunter, 2001), which resulted in higher complexity in the wine (Hunter & Fouché, 2000). In the case of the underdeveloped shoots, no difference was found in the phenol accumulation curves between the shaded and exposed canopies. The similar levels of PPFD received by the underdeveloped shoots in the shaded and exposed canopies after véraison (Chapter 4) could be the explanation for this.

No significant difference in the phenol content of berries from normally and underdeveloped shoots was found at any time after véraison. At five weeks it even seemed as if the levels in the underdeveloped shoots were a little higher (albeit not significant). It is, however, very possible that the flavour profile of these shoot types differ from one another, since the normal shoots received more sunlight than the underdeveloped shoots from the third week after véraison (Chapter 4).

Skin colour: The accumulation of precursors for anthocyanin synthesis was favoured at véraison (Hunter & Visser, 1988). During the ripening stage the colour increase was strongly correlated with the sugar levels in the berry skins (Hunter *et al.*, 1991b). According to Haselgrove *et al.* (2000) the anthocyanin levels per berry increased up to a ripeness level of 22 °B, whereafter it decreased with further ripening. This probably differs between cultivars, since the colour concentration seemed to have reached a plateau before a sugar level of 22 °B was reached. The highest anthocyanin concentration was reached about three to four weeks after véraison, depending on the level of shoot development and degree of canopy exposure. This is in accordance with Hunter *et al.* (1991b) who found the highest anthocyanin content in the berries 20 to 30 days after véraison.

Although no statistically significant difference in the colour intensity or density was found between the shaded and exposed canopies five weeks after véraison, it seemed as if the average levels were a little lower in the exposed canopies during the previous two weeks. This may possibly be due to a more gradual increase during the earlier stages of berry ripening. Both light exposure and temperature seemed to affect anthocyanin metabolism. It was generally found that light exposure, especially during the early stages of ripening (Haselgrove *et al.*, 2000), led to higher anthocyanin concentrations, while shaded conditions tended to induce low colouration (Archer, 1988; Smart *et al.*, 1988; Calò *et al.*, 1995; Keller & Hrazdina, 1996; Haselgrove *et al.*, 2000; Kliewer & Dokoozlian,

2000; Tomasi *et al.*, 2000; Bergqvist *et al.*, 2001). An increase in anthocyanins was found with an increase in temperature, but only up to a certain point, whereafter a decrease in anthocyanins with a further increase in temperature occurred (Coombe, 1987b; Bergqvist *et al.,* 2001). Too high temperatures during early berry ripening inhibited anthocyanin synthesis and/or increased anthocyanin breakdown (Haselgrove *et al.*, 2000).

The interaction between these two factors may explain any differences found in the colour concentration between shaded and exposed canopies. During the first week after véraison, when no difference in the light exposure was found (Chapter 4), the berry colour concentration of the canopies was similar. Possible higher berry temperatures in the exposed canopies could have induced inhibited anthocyanin synthesis and/or increased anthocyanin breakdown (Haselgrove *et al.*, 2000) that would have resulted in the lower antocyanin levels found in the exposed canopies during the third and fourth weeks after véraison. At five weeks after véraison the better sunlight penetration in the well-exposed canopies became more apparent and could have led to higher levels of anthocyanin production and accumulation, despite any possible inhibitory effects of higher berry temperatures.

The ultimate berry skin colour was related to at least three factors operating separately, namely berry sugar, cluster exposure and crop load (leaf area/fruit mass ratio) (Iacono *et al.*, 1994). Between the first and third week after véraison higher average colour concentrations were measured for berries from normally compared to underdeveloped shoots. Since no significant difference in the sunlight exposure (Chapter 4) or sugar content was found at that time, it was concluded that the crop load of the shoots played the most important role in the colour accumulation. Underdeveloped shoots could be regarded as over-cropped, with insufficient leaf area to adequately ripen their clusters (Peterson & Smart, 1975). This is supported by the sub-optimal total leaf area per gram grape berries found for the underdeveloped shoots (Chapter 6). This could be the explanation for the lower colour concentration found for the berries of the underdeveloped shoots, since over-cropping resulted in poor colouration (Bravdo & Naor, 1995). During the later ripening stage the increased berry temperatures due to the higher exposure of the clusters (Chapter 4) could have resulted in anthocyanin breakdown in the normally developed shoots. Although the average colour intensity and density measurements seemed higher in the berries of the underdeveloped shoots, it was not significant.

Before any conclusions on the grape quality based on the phenol and colour measurements can be made, the berry size (and thus the skin:pulp ratio) must also be considered. Since the most important factors contributing to the originality and quality of wines were localized in the skins, the best wines were obtained from grape varieties with small berries (Bidan, 1977). Bravdo & Naor (1995) found that small berries had a better potential for enriching the must, while Hunter (1991) stated that smaller berries due to cultivation practices had a higher skin:pulp ratio that resulted in an increase in wine quality. The reason for that is the higher surface area to volume ratio of the smaller berries that produced a more intense wine (Trought, 1996) with deeper colour and more flavour (McCarthy, 1996).

Larger berries with a lower skin:pulp ratio were found from underdeveloped than normal shoots at five weeks after véraison (Chapter 6). It was thus expected that berries from underdeveloped shoots would have lower anthocyanin and phenol concentration than those from normal shoots, based on the findings of Gray *et al.* (1997). However, no statistical significant difference in the concentration of these compounds (measured as absorbency units) was found between the shoots. Nevertheless, due to the thicker skins and higher skin:pulp ratio of the berries from the normally developed shoots, higher extractability potential during the wine-making process is assumed. It was therefore expected that wines made of grapes from normally developed shoots would be more flavoursome with better colour than those from underdeveloped shoots.

As already mentioned, underdeveloped shoots could be regarded as over-cropped with insufficient leaf area to adequately ripen their clusters (Peterson & Smart, 1975). Due to the sub-optimal total leaf area:berry mass ratio (Chapter 6) and lower photosynthetic rate per unit leaf area (Chapter 4), delayed berry maturation, poor colouration and low aroma and flavour were expected, based on the findings of Bravdo & Naor (1995). According to Koblet (1977) lower sugar, colour and phenol concentration were found in grapes from shorter shoots, while research quoted by Long (1987) showed that wine made from those grapes had low levels of ethanol, colour and phenol compounds. Despite that, a peculiar absence of significant differences in grape composition was noted between the grapes of the normally and underdeveloped shoots. This led to the assumption that the assimilates needed for berry ripening in the latter shoots originated in other organs than the leaves, such as adjacent shoots and the rest of the

permanent structure of the vine (cordons, trunk or roots). Koblet (1977) noticed that short shoots imported more assimilate from adjacent shoots than did normal shoots. Therefore the presence of short shoots in the canopy could be responsible for a decrease in the grape quality of the other, stronger shoots from the same vine.

The larger differences in berry size found between shoot types in the shaded compared to the well-exposed canopies (Chapter 6) might be evidence of this. Since the photosynthetic activity of shoots was lower in shaded than in exposed canopies (Chapter 4), the total carbohydrate production of the normal shoots in shaded canopies seemed insufficient to supply in the ripening needs of their own clusters and of the shoot itself as well as the ripening of stem tissue and clusters of the underdeveloped shoots in the canopy. This was illustrated by the lower levels of starch that accumulated in the normal shoots from shaded compared to that of exposed canopies (Chapter 1).

Although no apparent difference in the grape composition or quality was found between berries of normally and underdeveloped shoots, the possible detrimental effects on the quality of the yield from normally developed shoots and on reserve accumulation in the permanent structure of the vine should not be overlooked. Shoot heterogeneity in grapevine canopies should thus be avoided as far as possible.

6. CONCLUSIONS

In order to keep producing grapes and must of excellent quality, carbon allocation to the clusters must be optimised without detrimentally affecting growth and development in other parts of the vine (Hunter, 2000).

Shaded conditions in the canopy should be minimised, since it was found that it negatively affected yield (Calò *et al.*, 1995), delayed berry growth and ripening (Rojas-Lara & Morrison, 1989) and resulted in unbalanced must (Jackson & Lombard, 1993) that were unfavourable to wine quality (Smart *et al.*, 1989). These conditions can be brought about by ineffective canopy management practices or too vigorous vegetative growth. The latter is an indication of unbalanced vines where assimilates are mostly translocated to the vegetative parts of the vine, while the clusters are neglected (Hunter, 1991). Imbalances

between yield and vegetative growth are often used to explain variation in wine quality. Both over and under-cropping will result in delayed berry maturation (Bravdo & Naor, 1995).

The positive effects of canopy management practices were mainly noticeable regarding the acid content of the berries. No differences in the sugar concentration (°B), glucose or sucrose levels were found in the berries between shaded and well-exposed canopies. The higher titratable acid and lower pH values found in the exposed canopies (statistically significant for the normal shoots at five weeks after véraison) were mostly due to the higher average tartaric acid found in these berries. Since no difference in the malic acid content was found between the canopies, a higher tartaric:malic acid ratio was calculated for the berries in the exposed canopies, especially for those from the normally developed shoots. No significant difference in the phenol or colour absorbancies was found at five weeks after véraison.

Despite the absence of significant differences in the grape composition between shaded and well-exposed canopies, the importance of a lower pH and higher tartaric:malic acid ratio in the berries should not be ignored, especially in a warm grape growing country like South Africa.

A peculiar absence in significant differences between the grape composition and quality of normally and underdeveloped shoots was found. Small differences have been noticed, such as the lower titratable acid and higher pH found for the normal shoots due to lower levels of malic acid and the possibly more desirable acid composition for quality wine production. However, in general no statistically significant differences in the sugar concentration (°B), glucose or sucrose levels, total acidity or pH, malic or tartaric acid, phenol content or the colour intensity and density measurements were found between the berries from normally and underdeveloped shoots at five weeks after véraison. It had been established that underdeveloped shoots were over-cropped, since a sub-optimal total leaf area:berry mass ratio was found (Chapter 6). These shoots probably had insufficient leaf area to adequately ripen their clusters (Peterson & Smart, 1975). This led to the assumption that the assimilates needed for berry ripening in the latter shoots originated in other organs than the leaves, such as adjacent shoots and the rest of the permanent structure of the vine (cordon, trunk, roots). The larger differences in berry size found between shoot types in the shaded compared to the well-exposed canopies (Chapter 6) may be evidence of this.

Since the photosynthetic activity of shoots was lower in shaded than in exposed canopies (Chapter 4), the total carbohydrate production of the normal shoots in shaded canopies seemed insufficient to supply in the ripening needs of their own clusters and of the shoot itself as well as the ripening of stem tissue and clusters of the underdeveloped shoots in the canopy. This was illustrated by the lower levels of starch that accumulated in the normal shoots from shaded compared to that of exposed canopies (Chapter 1).

Although no apparent difference in the grape composition or quality was found between berries of normally and underdeveloped shoots, the impact of underdeveloped shoots on the quality of the yield from normally developed shoots and on reserve accumulation in the permanent structure of the vine should not be overlooked. Shoot heterogeneity in grapevine canopies should thus be avoided.

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CHAPTER 8

GENERAL DISCUSSION AND CONCLUSIONS

International competition between wine producing countries force producers to produce the best possible grape quality without impairing vegetative growth and development in other parts of the vine or decreasing the amount of reserves stored for initial growth in the following season and vine maintenance.

According to Carbonneau (1995) the microclimate, yield, berry maturation and wine quality are dependent on the canopy structure. The microclimate inside grapevine canopies can be defined as the signal for physiological functioning (Smart *et al.*, 1985a) and depends on the amount and spatial distribution of the canopy structure.

Too dense canopies are detrimental to the physiological functioning of the vine, since the photosynthetic efficiency of individual leaves (and per implication whole vine photosynthesis) is closely linked to the amount and intensity of sunlight interception (Hunter, 1991). It is therefore important that the maximum number of leaves is exposed to the environment, so that each leaf can contribute to the photosynthetic capacity of the vine (Archer, 1988). A way to accomplish that is through the practice of canopy management.

Canopy management practices during the growth season are aimed to change the magnitude, position, and/or orientation of canopy components (shoots, leaves and clusters) to improve the microclimate (light, humidity, air flow, temperature) and to balance the vegetative (including the roots) with the reproductive development and functioning (Hunter & Archer, 2001). Carbon allocation to fruit sinks can thus be optimised (Hunter, 2000), while longevity of the vine is still maintained.

The composition (and thus the quality) of the yield is usually described as a mean value (Trought, 1996), although a large variation around the mean may exist. Then, even though the average composition may seem acceptable (Trought, 1996), the potential for the presence of overripe as well as unripe flavours in the must and wine is increased. Smart *et al.* (1990) stated that high quality wines probably resulted from processing grapes of relatively homogeneous composition, which may be obtained through canopy management practices that induced uniform sunlight interception throughout the whole canopy (Volschenk & Hunter, 2001).

Apart from the effects of sunlight exposure (as also mentioned by Coombe, 1987b), asynchronous ripening may be enhanced by the varying leaf area:fruit ratio of individual shoots (Jackson & Lombard, 1993). Peterson & Smart (1975) mentioned that short shoots might have insufficient leaf area to adequately ripen their fruit. In order to ripen their clusters, Koblet (1977) found that short shoots imported more assimilate from adjacent shoots than did normally developed shoots. Grapes from the shorter shoots showed nevertheless a slight reduction in sugar concentration as well as a reduction in colour and phenols. The assumption could thus be made that the presence of short shoots could be responsible for a decrease in the grape quality of the other, stronger shoots from the same vine and in this way affect the quality of the total crop. Too long shoots represented the diversion of photosynthetate into a superfluous leaf area, which in turn contributed to canopy shading (Smart *et al.*, 1990), while optimum ripeness of the clusters could not be attained (Archer, 2001).

According to McCarthy (1996) high quality wine generally came from vines with a moderate vigour. Archer (2001) found that shoots of a medium length (±120 cm) produced the best grapes for making quality wine, compared to the sub-optimal ripening of grapes (and thus poorer wine quality) in the case of long (>200 cm) and short (±60 cm) shoots. It was further found that shoots with an average length of 145 cm produced wines with higher tannin, anthocyanin and alcohol content than grapes from 110 cm shoots (Nadal *et al.*, 2001).

Different shoot lengths in a vine would thus lessen the overall quality of the yield (Archer, 2001), while equality in shoot growth seems important for the production of homogeneous, top quality grapes. The eventual objective of canopy management is to obtain a photosynthetic efficient, homogeneous canopy with uniformly and well distributed shoots of similar vigour, producing healthy, high quality grapes of similar bunch and berry size and with a uniform level of ripeness (Hunter & Archer, 2001).

Even though canopy management practices are widely accepted and executed as a rule during grape cultivation, large heterogeneity in shoots growth still exists in standard vines (Smart, 1988). A large proportion of underdeveloped shoots with smaller leaves, fewer secondary shoots, shorter internodes and a lower leaf area:shoot length ratio than normal shoots, were found by Smart in canopy interiors where they developed poorly in the shaded conditions. According to Archer (2001) shorter shoots tended to develop in the middle of longer cordons,

while over-long shoots were mostly found at the end of cordon arms and close to the split of the cordon.

The purpose of this project was to investigate the effect of shoot heterogeneity in a Shiraz/Richter 99-vineyard on vegetative and reproductive growth parameters, vine physiology and grape composition and at the same time enable the producer to better understand the physiology of the vine and the importance of homogeneous shoot development in a vineyard.

The higher total number of shoots and thus more shoots per metre cordon that were found in the shaded compared to the exposed canopies were ascribed to the suckering procedure that was carried out in the latter. A lower percentage normally developed shoots and higher percentage underdeveloped shoots also occurred in the shaded than the exposed canopies, which were explained by less translocation to each individual shoot due to the higher shoot number. Due to the constantly lower PPFD received by the underdeveloped than the normally developed shoots in both the shaded and well-exposed canopies, it was concluded that the underdeveloped shoots were situated more to the canopy interior. The low PPFD received by the basal leaves of the shoots, the possibility of insufficient leaf area per shoot to induce fruit primordia, as well as the possible effect of sub-optimal starch accumulation in the spurs during the previous growth season were all are factors that were discussed as feasible explanations for the low level of fertility found in the underdeveloped shoots. The shaded canopy interiors could also have resulted in the lower percentage fertility found for the normal shoots in the shaded canopies.

Since a greater extent of shoot heterogeneity was noted for the shaded than well-exposed canopies, asynchronous berry ripening with more variation in the composition was expected. Due to the connection already made between the uniformity of berry ripening and the wine quality (Smart *et al.*, 1990), the wines made from the clusters in the shaded canopies are more likely to be lower in quality compared to the wines from the exposed canopies.

It was found that normally developed primary shoots were longer and thicker than underdeveloped shoots, with more and longer secondary shoots distributed over the whole length of the primary shoot. The latter is according to literature important for the optimal efficiency of the canopy (Hunter, 2000). Significantly larger primary leaves were found on normally than underdeveloped shoots,

although no difference in the number of leaves per shoot was found. Normal shoots had more and larger secondary leaves than underdeveloped shoots, with the result that the total leaf area of normal shoots comprised of primary and secondary leaves in an approximate 1:1 ratio. Exposed canopies seemed to promote secondary shoot and leaf development in especially the normally developed shoots. Normal shoots could thus have the potential to produce a higher yield with better quality than underdeveloped shoots, due to the more desirable leaf area composition supplementary to the larger total leaf area per shoot.

In the first five weeks after véraison photosynthesis, transpiration, stomatal conductivity and WUE decreased as berry ripening progressed, while the internal CO_2 levels in the leaves increased. This was mainly ascribed to an increase in leaf age of the basal leaves and consequent change in internal anatomy and functionality, decreased demand for assimilates by the vine, decreased PPFD and an increase in water stress.

The positive effect of canopy management practices on the physiological activity of the leaves only became apparent in the third week after véraison. Although none of the following differences were statistically significant (except for the photosynthetic activity at five weeks after véraison), leaves on shoots in well-exposed canopies received higher levels of PPFD, displayed higher rates of photosynthesis and transpiration with lower stomatal resistance and lower internal CO_2 levels. Diurnal cycles monitored in the fifth week after véraison showed that higher maximum levels of PPFD (with more uniform light penetration), photosynthesis, transpiration and stomatal conductance were measured in the exposed than shaded canopies between late morning and early afternoon.

The difference in physiological activity between leaves from normally and underdeveloped shoots also became only apparent in the third week after véraison when normal shoots displayed significantly higher rates of photosynthesis and transpiration than underdeveloped shoots. Likely reasons discussed were the lower source:sink ratio of the underdeveloped shoots as well as a possible physical resistance against gaseous transfer in the leaves from those shoots. Normal shoots further received higher PPFD levels, while higher stomatal conductance and lower internal CO_2 levels of the leaves were measured than in the case of underdeveloped shoots. A higher WUE ratio was

also calculated for the normal shoots. According to day cycle measurements, the most apparent differences in the physiological activity between normally and underdeveloped shoots in shaded and well-exposed canopies occurred from 10:00 to 14:00, the most significant being at 12:00. Higher stomatal conductance, transpiration rates and significantly higher photosynthetic rates were measured at midday for the normal compared to the underdeveloped shoots. The physiological functioning of the normal shoots also seemed to be more efficient in terms of water relations, since higher WUE was calculated between 10:00 and 14:00.

No positive correlation between the photosynthetic activity and the chlorophyll concentration of the leaves was found at five weeks after véraison. Although higher levels of chlorophyll *a*, chlorophyll *b* and total chlorophyll ($\mu g.g^{-1}$) were found in leaves from underdeveloped compared to normally developed shoots, equal amounts of chlorophyll.cm^{-2} and a non-significant difference in the assimilation number ($\mu mol.\mu g^{-1}.s^{-1}$) were calculated for the leaves from these different shoot types. It was not clear how important the effect of canopy exposure was on the leaf chlorophyll content, since different results were obtained in two consecutive years.

The physiological functioning of leaves from normal shoots was found to be superior to those on underdeveloped shoots. Since it was further taken into account that normal shoots had significantly more total leaf area per shoot than the underdeveloped shoots, it was assumed that the total carbohydrate production by normal shoots would also be significantly higher. As the grape berries are the most important sinks for assimilates during the ripening period (Koblet, 1977), it is expected that the size and quality of the yield from normally developed shoots will be higher than that from the underdeveloped shoots.

Clusters on normally developed shoots were significantly larger than those on underdeveloped shoots with significantly more berries per cluster. Factors such as light exposure, crop load and carbohydrate supply to the clusters were discussed as possible reasons for this. The growth and ripening curve of the berries from underdeveloped shoots seemed to have been delayed because of over-cropping of the shoots. Together with the larger berries and smaller skin:pulp ratio found for the underdeveloped shoots, it was expected that berries from normal shoots would be better ripened with more intense flavour and colour.

The cluster size was probably affected before véraison during the vegetative growth phase of the shoots, since no further increase was noticed in the weeks after véraison. Although the degree of canopy exposure did not affect the cluster size significantly, it seemed to have had an effect on either the berry set or the berry size of clusters, depending on the level of shoot development. It seemed as if the berry size of the normal shoots were a little larger in the exposed than in the shaded canopies, albeit not significant. Despite the smaller berry size and higher skin:pulp ratio of the berries in the shade, better composition and quality than the berries in the exposed canopies were not expected as the smaller berry size was attributed to impaired carbohydrate nutrition during the second rapid growth phase of grape berries. Canopy management practices should further improve the berry quality of the normal shoots. Better exposure of the canopies did not affect the berry size of the underdeveloped shoots, but rather the number of berries per cluster and thus the cluster size and yield.

The positive effects of canopy management practices on grape composition were mainly noticeable regarding the acid content of the berries. The higher titratable acid and lower pH values found in the exposed canopies (statistically significant for the normal shoots at five weeks after véraison) were mostly due to the higher average tartaric acid found in these berries. Since no difference in the malic acid content was found between the canopies, a higher tartaric:malic acid ratio was calculated for the berries in the exposed canopies, especially for those from the normally developed shoots. No significant differences in the sugar concentration (^{o}B), glucose or sucrose levels as well as in the phenol or colour absorbancies were found in the berries between shaded and well-exposed canopies. Despite the absence of statistically significant differences, the importance of a lower berry pH and higher tartaric:malic acid ratio should not be ignored in a wine producing country like South Africa. Gradual development and ripening of berries on normal shoots and in exposed canopies presents the opportunity for selective harvesting and wine style.

Even though large differences in the total effective leaf area, crop load and physiological activity per unit leaf area was found between normally and underdeveloped shoots, no statistically significant differences in the berry composition was found at five weeks after véraison. As it was found that lignification of underdeveloped shoots occurred later in the season than normally developed shoots, competition between shoot and berry ripening most probably occurred. Lower levels of starch formation and accumulation also occurred in the

underdeveloped shoots, while the reserves were more evenly distributed over the whole length of normal shoots. In order to maintain longevity of the vine (and also the individual spurs), grape ripening should occur without any detrimental effect on other processes in the vine, such as reserve accumulation. This did not happen in the case of the underdeveloped shoots, as reserve accumulation seemed to be impaired by grape ripening processes.

Except for the competition between berry ripening and reserve storage, it was also believed that the assimilates used by the underdeveloped shoots for cluster ripening might have originated in other organs than the leaves, such as adjacent shoots and the rest of the permanent structure of the vine (cordons, trunk or roots). The larger differences in berry size found between shoot types in the shaded compared to the well-exposed canopies could be evidence for this. Since the photosynthetic activity of shoots was lower in shaded than in exposed canopies, the total carbohydrate production of the normal shoots in shaded canopies seemed insufficient to supply in the ripening needs of their own clusters and of the shoot itself as well as the ripening of stem tissue and clusters of the underdeveloped shoots in the canopy. This was illustrated by the lower levels of starch that accumulated in the normal shoots from shaded compared to that of exposed canopies.

The study clearly showed that shoot heterogeneity results in uneven vegetative and reproductive growth, physiological activity as well as reserve accumulation in the vine. Underdeveloped shoots act as parasites in grapevine canopies by importing assimilates from adjacent normally developed shoots and the permanent vine structure in order to ripen their clusters. Berry and shoot ripening of normal shoots as well as starch accumulation are thus detrimentally affected. Shoot heterogeneity should therefore be avoided in commercial vineyards.

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